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COMMUNICATION AND RELATIONSHIPS IN THE GENUS *Tyrannus*

PUBLICATIONS OF THE NUTTALL ORNITHOLOGICAL CLUB

EDITORS, OSCAR M. ROOT AND RAYMOND A. PAYNTER, JR.

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by

W. JOHN SMITH

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INTRODUCTION AND DISPLAY BEHAVIOR OF *TYRANNUS TYRANNUS*

Chapter 1.

INTRODUCTION

This study, the first of several to be published on my continuing program of studies of the family Tyrannidae, is confined to the type genus. Ethology, ecology, and zoogeography are each discussed, and the taxonomic implications of the findings suggested, but the main theme of the report comprises an analysis of the nature and integration of the display behavior of each species, and its adaptive significance. To this end one species, *Tyrannus tyrannus,* is presented in considerable detail in an attempt to show how its displays are used to cope with the communication demands placed upon the species by its life history and environment. The displays of the other species are then compared to those of *T. tyrannus,* in order to reveal the similarities and differences in patterns of communication found among congeners that differ both in their environments and in some aspects of their life histories.

The family Tyrannidae is a large, loosely defined phylogenetic assemblage of New World suboscine passerines referred to collectively as "flycatchers." However, while the species of the genus *Tyrannus* do for the most part forage by flycatching (aerial pursuit or flight gleaning of invertebrate prey), many members of the family are much less aerial, and even may be largely frugivorous. The Tyrannidae show an amount of adaptive radiation unparalleled in most other continental families and exceeded only by such insular groups as the Drepanididae of Hawaii or the Vangidae of Madagascar, yet at the same time they contain large groups of morphologically very similar species. These groups have become specialized to such diverse modes of life as to resemble not only the Old World flycatchers, but also titmice, larks, wagtails, shrikes, thrushes, swallows, warblers, and vireos. Despite this, the groups are not separated from one another by obvious gaps, and nearly complete sets of intermediate species connect the adaptive extremes, a feature that has made the taxonomy of the family a matter of much dispute.

It was because of their immensely interesting biological radiation that I began to study the Tyrannidae, and one of the first goals I set was to gain a better understanding of taxonomic relationships within the family — i.e., to determine the evolutionary history of the adaptive radiation. This radiation had resulted in a wide range of form in each of the structural features used as bases for earlier supraspecific taxonomic schemes, but those structures were mostly trophic and motor, and probably among the most evolutionarily labile that systematists could have chosen. To study the selection pressures that might have been operating on bills, tarsi, wings and tails I observed the habitat and feeding ecology of tyrannids. To obtain additional characteristics of possible taxonomic use, I studied plumage patterns and display behavior. The problem of understanding the functioning of the displays soon became foremost, and eclipsed the other endeavors. Yet, while I feel that what has been learned about the means by which these birds communicate is the most exciting part of the story, I do not mean to suggest that it has not in addition served my original intent. A knowledge of the displays has been useful in showing relationships among the various species, and, taken with other information, sheds some light on the radiation that has taken place within this genus. On a broader scale, what has been learned about this and other genera is aiding me in a general reassessment of the taxonomy of the family.

GENUS *TYRANNUS*

The included species are large flycatchers with overall lengths of about eight to nine inches (longer in the subgenus *Muscivora,* in which the two species are relatively small but have very long forked tails).

There are two basic color patterns in the subgenus *Tyrannus:* (1) white below and gray or black above (also characteristic of the subgenus *Muscivora,* although one species has salmon-colored areas), and (2) yellow below with olive or brown, gray, or greenish usually tinged with olive above, and usually some or much gray on the head. The species with these two different sorts of coloration can also be subdivided on the basis of zoogeography. All species have a bright yellow, orange-yellow, or vermilion red patch of feathers concealed in the center of their crowns.

Species may be either sedentary or migratory, or have different populations which are one or the other. They range over most of the New World, from the Arctic Circle in the northwest, to the Rio Negro in Central Argentina. Outlines of species' ranges presented herein are taken primarily from Hellmayr (1927), Eisenmann (1955), and Godfrey (*in press*) with some recourse to other accounts more recent than Hellmayr, and to personal experience. My descriptions of ranges are intended to be only as detailed as necessary for present purposes. I have followed Hellmayr for species' names except where otherwise noted (see Chapter 11).

METHODS

Collection of Data

Research has been based on field observations supplemented by laboratory analyses. All of the birds observed have been wild, free ranging individuals, with the exception of two hand-reared young. Field work has occupied various seasons in each year from 1959 to 1965 in parts of North, South, and Middle America, and the West Indies. In most seasons more than one species of *Tyrannus,* and often flycatchers of other genera, were studied simultaneously. One result of this was the accumulation of a considerable body of material for inter-individual and inter-species comparisons. A less desirable result was a lack of continuity, and the need to pool observations made on different birds to obtain a picture of seasonal progression. The study originated, however, as a general review of the Tyrannidae with taxonomic ends, and this dictated certain features of its design. Fortunately, many published descriptions of the breeding biology of at least the North American species already exist and can be used to augment what I learned. While good data on many such things as incubation period and nest structure can be found, the descriptions of display behavior and its occurrence are almost always so incomplete, vague, or anthropocentric as to be of little ethological help.

In observing kingbirds I never found it necessary to use a blind. The birds did not usually give any indication of being disturbed when watched from distances of 50 yards or so through eight- or ten-power binoculars. This was fortunate, for using a blind would have restricted my field of vision, and most flycatchers, especially kingbirds, are highly mobile. In order that the birds would not recognize me as a predator, I rarely investigated the contents of a nest and thus could not always know precisely the stage a pair had reached in the breeding cycle. Further, I did not attempt to capture and mark individuals, again so that the pair would not recognize me as a dangerous feature of their environment.

Although in most situations I could quickly determine the sex of each member of a pair because each sex has relatively fixed roles, it was nonetheless inevitable that encounters between unidentified individuals would be observed. This commonly happened when an intruding individual was fighting one member of a pair, and it was a particularly important and persistent problem in early spring before nests had been built, and late in the year when families comprising both parents and fledglings were active. This inability to identify the sex of a particular individual at all times has left its mark on few situations; these will likely be resolved only by further study, with marked birds.

Sometimes I was able to use birds that were naturally marked, such as individuals that had lost conspicuous wing or tail feathers. Some observers (e.g. Skutch, 1960) have marked individuals. Their findings, taken together with the fact that only females of the genus are known to have incubation and brood patches, permit a certain confidence in assigning sex to a bird consistent in a certain role. Finally, one peculiarity of plumage occasionally enabled me to make a determination of sex observationally. Males of all of the species except *T. caudifasciatus* have tips to the outermost primaries that are much more emarginated than are those of females, and these tips were sometimes clearly visible when a bird stretched or preened a wing. On a very few occasions I was able to tell the degree of emargination from a frame of movie film.

Throughout this paper, whenever the sex of an individual is assumed without comment it is because the bird consistently behaved in a manner that I feel is characteristic of the role of one sex only. These consistent mannerisms were of the following sort: in any pair, the male was more aggressive toward all conspecifics including its mate. Males also consistently perched near the nest sites while their mates did all the building, and similarly perched "guarding" during the incubation and brooding period, especially when the female was off the nest foraging. When a male might occasionally gather a bit of material and bring it to the nest or to some perch close to the nest while the female built, he would always drop it ineffectually without trying to work it into the nest. Only one pair member, the female, incubated and brooded, and although both parents fed the nestlings, the female usually did more than her mate.

Field notes were taken on habitats, nesting sites, and feeding behavior, as well as on communicating behavior, but the last received by far the greatest part of my attention. Until 1962 I wrote down field notes as I observed, but this process is wasteful of detail and requires frequent interruptions in observation. From that point I began to dictate observations into a small, portable tape recorder, and was able to preserve much more detailed accounts of longer sequences of behavior. Even this method, however, is wasteful of detail, for details cannot all be grasped as they occur, nor can the sequence of events always be dictated sufficiently rapidly to keep up with the birds. In 1960 I had attempted to grapple with this problem by filming encounters, but found that the problems inherent in managing a 16mm cine camera seriously interfered with my ability to follow the birds.

In 1964 I began to use an 8mm zoom lens reflex camera with automatic exposure control. This instrument can be used without a tripod, and was much less trouble to handle than the earlier 16mm equipment. It was usually operated by my wife while I operated other equipment, and we kept the dictation tape recorder running throughout our observations. The technique permits repeated reviewing of the filmed events and appears to be promising, but of the species covered in this report it was used extensively on only the Scissor-tailed Flycatcher.

The most important instrument employed in the field was a high fidelity tape recorder with its microphone set inside a parabolic reflector. In the first season it became clear that many if not most of the important displays of tyrannids are vocal, and in many species these are extremely difficult to transliterate. In fact, as Thorpe (1959) has discussed in some detail, it is impossible to characterize bird sounds accurately using our alphabet. Where I have used vowels and consonants below to attempt to render the sound of a bird vocalization it has been only to provide a rough approximation of the sound.

In 1960 I began to record tyrannid vocalizations on magnetic tape, using a portable Magnemite recorder with an Electro-Voice model 650 microphone mounted facing a 30-inch diameter parabolic reflector. The recorder is a poor one with many important limitations, but the results were sufficiently encouraging that in 1961 I made more extensive use of the same equipment, and then switched to a Nagra III-B tape recorder with an AKG Stud-S omnidirectional microphone mounted facing a 39-inch diameter parabolic reflector. This equipment was used, more and more extensively, throughout the remainder of the work. In all cases, recording was done at a tape speed of 15 inches per second.

Analysis of Data

Bird sounds comprise structures too detailed to be abstracted by the human ear, although their intricacies may be more available to the avian ear if Pumphrey (1958, 1961) is correct in estimating that the latter may be able to respond to changes in amplitude and frequency in one-tenth the minimal time span required by the human ear. Various sorts of analysis of the physical properties of sound are possible, and for a full understanding of the form of vocalizations several are probably required. A method of describing the distribution of frequency in time (much as music is scored) with at least some indication of relative loudness is perhaps the most useful single mode of analysis, however, and is the one employed in this study. The results of such analyses, presented in the form of "audiospectrographs" or sonagrams, have been used to illustrate examples of the vocalizations of which I have recordings. Many thousands of sonagrams have been prepared and studied in addition to those shown. The studies were prepared on three different machines, all built by the Kay Electric Company, and all of the same basic design. These were a 661-B Sona-Graph (used at Massachusetts Institute of Technology), a 675 Missilizer (used at Harvard), and a 6061 A transistorized Sona-Graph, now installed in my own laboratory. These three instruments all performed the same job, and analyses from each are directly comparable, but all illustrations of sounds used in this report have been copied from traces made on the model 6061 A.

The analysis has resulted in the recognition of a set of displays for each species, and I hold that these displays are the ritualized signals with which members of the species communicate. In keeping with ethological convention, each display has been given a name, and this is capitalized. I have attempted to choose names that would permit the broadest possible recognition of inter-species homologies.

Many of these names are rather awkward. Although simpler names, for instance rough onomatopoetic copies of the vocalizations, could doubtless have been chosen, these would have been poorer currency in a comparative study. The range of usage of each display has been indicated, and examples of observed behavior sequences have been included where it was felt that these would enable better understanding.

Interpretation

For each display a message and a partial set of meanings have been inferred. The message is the information encoded in the signal that is descriptive of some aspect(s) of the central nervous state of the communicator. The features of the message that identify the communicator in various ways are determined by comparing the display with the repertoires of other birds, thus revealing differences between species and individuals. Differences between sexes also appear, sometimes because females rarely or never use particular displays. Additional message features are inferred by studying all of the various situations in which a display is used and, insofar as possible, the subsequent activities of the bird that used the display. The common denominator of these cases that appears to describe the communicator's state at the time of communicating is taken to be part of the message.

The meanings in the system under study are, on the other hand, peculiar to the recipient in the communicative event (see Smith, 1965), and result from the recipient's placing the message in its total relevant context. Meanings are interpreted in the *ideal* case from the response of the recipient to the signal (from Cherry, 1957: the response which the recipient chooses from all of the possible responses is taken to be the meaning of the signal to the recipient). Unfortunately, the complexity of a biological system involving such advanced animals as birds makes the *ideal* method almost always impossible; the recipient may make no overt reaction or may react on the basis of the past several meanings it has obtained; the context can be enormous and is very difficult to know in full. The context may include not only other events concurrent with or recently preceding the signal, but also remembered events and inherited predispositions.

In most cases, the observer must infer the meaning in any particular situation from the message and his understanding of the possible functions this message could have within the social organization of the species in question, in the observed context(s). Since most messages occur in more than one context, they are capable of generating more than one meaning, and there can be overlap between the meanings of different displays. The system comprising communicator, message (encoded in a signal, or display), recipient, context, and meanings is further discussed later, following presentation of the form and usages of the displays of *T. tyrannus*.

This emphasis on the analysis of message and the inference of meanings is thought to represent a new approach to the interpretation of animal communication, although other, related work applying semiotic principles has been begun by Marler (1961), and the field has been discussed by Sebeok (1965). Use of a new form of analysis is fraught with the dangers of semantic misinterpretation, and to ease the possibility of confusion I have appended a glossary which includes both stipulative definitions proposed for this report and some of the more standard ethological terms. The basic assumption involved in the genesis of this interpretive technique has been that natural selection will act on the communication system of any species to obtain signals encoding messages about *any* features of an individual's central nervous states (loosely, its "mood") which can generate socially usable meanings. There will be various sorts of limits and counterselection pressures, of course (e.g., the kinds of signals are restricted by the characteristics of the species' transmitter organs which usually have additional, non-signal functions, and signalling animals become more conspicuous to predators), although these need not be discussed here. One important point is that while some messages (such as anger, or identifying information) are obvious candidates for encoding, other messages may not be *a priori* anywhere nearly so obvious. The material upon which natural selection acts must, in the last analysis, originate by chance, and any message which in the appropriate contexts can generate usable meanings has some chance of being maintained. Conversely, messages that might be extremely useful may never get the chance to be encoded. A more thorough discussion of the implications of evolutionary theory for message/meaning analyses is presented in Smith (*in press*).

Apart from this emphasis on analysis for messages and meanings, the fundamental methods of interpreting displays do not depart to any extent from the established procedures of ethological research. The functions of displays have usually been inferred from the immediate and extended behavioral and environmental contexts in which the displays have been observed. In the case of visible displays, which are often divisible into components that recur in other displays, the components have been studied and compared in each usage. Visible displays are often similar to movements and postures occurring in nonritualized locomotion, pecking, or peering, for example, and inferences based on such comparisons are commonly used. Descriptions of these and similar methods have been presented in greater detail by various authors (see, for example, Moynihan, 1955, and Tinbergen, 1959).

T. TYRANNUS AND THE ANNUAL CYCLE OF BEHAVIOR

The Eastern Kingbird is the most contrastingly marked bird in the genus. It is basically slate black above and white below, with pattern provided by a white tip to the rounded tail, very narrow white edges to the outermost rectrices, and white edgings to some of the wing coverts. A brilliant but concealed patch of orange-red in the center of the crown lends the only color to the plumage. In plumage pattern, coloration, and size, males and females are essentially identical — a feature characteristic of all but one member of the genus, *T. forficatus.*

Geographically, *T. tyrannus* is one of the most widespread species, and breeds northward to about the limit of the Boreal Forest Region (see Rowe, 1959) in Canada except in the Yukon and most of Quebec. Its northern limit in the east is in southern Quebec and the Maritime Provinces (for greater detail see Godfrey, *in press*). It is casual even north of this, and in the west may breed to the Arctic Circle at times — e.g., S. D. MacDonald and I saw a pair in 1958 by a lake near Norman Wells, N.W.T., about 100 miles south of the Arctic Circle. Southward it extends through suitable habitat to the Pacific Coast around Vancouver Island and Seattle, and down the mountains to northern Nevada and New Mexico; it is found in the central United States south to central Texas and in the east breeds to southern Florida. Migrating through Central America it winters primarily along the Andean chain from somewhat south of Colombia to approximately southern Bolivia. It is a very rare migrant or vagrant in the Bahamas and Greater Antilles, and is unknown in the Lesser Antilles.

My first, and most intensive, season of field work with *T. tyrannus* was spent at the Delta Waterfowl Research Station, Delta, Manitoba, from 16 May to 2 August, 1960. In subsequent springs (1961, -62, -63, and -64) I spent from one to several days at irregular intervals working with the species at the farm of Dr. and Mrs. Ernst Mayr, near Wilton, New Hampshire. In 1963 and 1964 many observations were made on a pair at Great Meadows Wildlife Reserve near Concord, Massachusetts, and in 1965 on two pairs at the Tyler Arboretum near Lima, Pennsylvania. Scattered observations have also been made at other points in Massachusetts, in Ontario, and in Pennsylvania. Only in 1960, at Delta, did I follow individuals nearly daily through the time from arrival on the breeding grounds until after the period of fledging. Unfortunately, this was the first year I used tape recording, and I did not use it extensively. In many ways it was the best field season I had with this species, for the population at Delta is extraordinarily dense. The lowest density with which I worked was in New Hampshire (two pairs, usually not within hearing distance of one another, almost no interactions). Several pairs were present at Great Meadows, but they were well spaced and did not usually interact.

In most respects the annual behavior cycles of this and other kingbird species are similar, and what differences there are relate primarily to the permanence of social bonds, the length of season available for breeding, and sometimes to other environmental influences. Only the cycle of *T. tyrannus* will be presented in detail; cycles of the other species will be compared and contrasted with it.

As behavior patterns change seasonally the communicational patterns of the species also change. For instance, most kingbirds are loosely associated or solitary in the non-breeding seasons, and so little dependent on one another that there is then little or no need of communication. As annual hormonal changes prepare individual birds for breeding, though, inter-individual behavior must be mediated; social relationships between mated individuals, rivals, parents and offspring, and others must be established and maintained. Particularly where this must all be done rapidly, as in migratory species, patterned communication is a necessity. Even members of resident species, although they may not have to establish either new pair bonds or new territories and have less need to communicate, are in this season faced with increasingly complex social interactions. Unlike migrants, such resident birds may maintain their pair bonds and territories the year-round and thus have to do some communicating even in the non-breeding seasons.

T. tyrannus is a migratory species. In the autumn of each year Eastern Kingbirds travel south, probably in small to medium sized, loosely coherent flocks (e.g., Darlington, 1931, and Wallace, 1958, in Colombia, and Eugene Eisenmann, pers. communication, in Panama). Through the winter and into the spring migration the species may remain divided into flocks or groups of a few individuals which apparently associate only loosely and quite quietly (personal observations in Panama in March, reported for Central America by Skutch, in Bent, 1942, by Crandall, 1914, and Slud, 1964, for Costa Rica, by Huber, 1932, for Nicaragua, and by Russell, 1964, for British Honduras). While flocks numbering up to one hundred are reported from tropical areas during April, birds arriving on the breeding grounds usually appear to be alone and unmated.

Males arrive in the north at least a few days before females in the regions where I have studied the species. Within a day after the males arrive, they begin to patrol loosely defined territories (see glossary). For at least the next few days, and especially, but not solely, in places of high population density, they are very active and very vocal. As more and more males arrive and settle, the sizes of the earliest territories are gradually pared down during considerable fighting. Yet neither this species nor any member of the genus appears to make use of a number of "song posts" on the territory as do some of the oscines (indeed, there is no single display which corresponds in all respects to what is usually called oscine advertising "song"), and there is little to suggest that boundaries ever become narrowly defined between neighboring males. I often saw intruding conspecifics deep within the territory, even in regions where breeding pairs were few. Such intruders would at times come to the nest and be attacked by one of the owners, but, through the early nest-building stages of the cycle an intruding conspecific individual might be tolerated in or near the nest tree if it did not display. Later, when there were nestlings, single intruders were seen near nearly all of the nests observed; these may have been what Skutch (1935) calls "helpers at the nest," birds apparently so strongly attracted to the nest or young that they intrude in spite of frequent aggressive responses by the owners. Early in the season, on the other hand, many disputes between males are cases in which an intruder persistently comes, not to vie for territory, but to approach a pair and attempt to mount the (presumed) female, only to be attacked by her mate.

The territory of the Eastern Kingbird (and perhaps in all *Tyrannus* species) is not fixed by its boundaries, in fact, but by the position of the nest or nest tree. Its early, larger size appears to shrink, much as Johnson (1963) has described in *Empidonax,* another tyrannid genus. In at least some instances (see Davis, 1941) kingbirds hold no obvious territories until after pair formation.

Pair bonding takes place shortly after the arrival of potential mates. Basically, bonding appears to involve the common avian method in which the initiative is with the female; she comes to the male and remains in his vicinity, even though he at first responds aggressively to her approaches. The female continues to take much of the initiative once the pair bond has formed. Only females build nests, although males have an activity (probably a display) that looks like nest site showing, in which a male squats and wriggles in various suitable crotches, vocalizing, while a female follows attentively. Many of my observations of this have been made when I could not be entirely sure of the sexes of the participants, although I do have several cases in which the site showing individual could be known by other behavior to be a male. A somewhat similar display has been described for a presumed male *Empidonax minimus* by Nero (1959), and a display similar in part but apparently not in the nest-forming movements for other *Empidonax* species males by Johnson (1963). Often the showing individual faces more or less toward the other individual. As nests usually do not seem to be constructed subsequently at such sites, I suspect the activity may be a display primarily relevant to pair-bonding. It is difficult to distinguish, however, from the behavior of a female who appears to be nest site prospecting, and cannot be fully understood until observations are made with marked individuals.

Females sometimes begin investigating crotches after such a performance by a male, and may search in several trees and over a period of days. In fact, one or two nests may be quickly built and abandoned before the final site is chosen. A male usually stays close to the nest site and watches while his mate does all of the building, and may (rarely) repeat his nest site showing in the nest itself (also seen in *T. couchii*). Males do not incubate or brood, and lack incubation patches. During the time of incubation and the brooding of very small nestlings, males show considerable interest in the nest, and usually "guard" from some convenient perch during absences of their mates. Females, however, do not permit their mates to come even to the rim of the nest at this period. Later, males share in some part of the feeding of nestlings and fledglings. The latter follow their parents about for some weeks after fledging, but gradually begin to elicit more and more aggressive responses to their approaches until by the time of fall migration family groups adhere only loosely, if at all.

T. tyrannus is an alert, almost hyperactive, bird. Individuals hunt alone, often taking a high, conspicuous perch from which they scan the surrounding air space for passing insects. Like other tyrannids, they often come down to lower perches and scan the foliage, from which they obtain prey by flight gleaning, or feed on fruits. But their habit of spending so much time in conspicuous places, and their quick reactions and agile maneuvering as they chase elusive prey, are the features particularly characteristic of these birds. Kingbirds, to a considerable extent all of the species, are birds that appear to "live by their wits." They are quick to interact socially, quick to flash aggressive responses, quick to attack a potential predator of their young, and unlikely to hide or to sulk. It is this temperament that permits them to position their nests conspicuously and almost carelessly, for they are ready and persistent in defense against predators. The same temperament may also, however, make difficult the adjustment of individuals to each other, and probably underlies the need for the rather large amount of communicative behavior in which they indulge.

At the start of the breeding season, when a male is staking out his territory, he is much more aggressive than is a female. He gradually becomes less aggressive once a pair bond is formed and may be least aggressive while the female is incubating. Throughout the season, however, he tends to become highly aggressive in both twilight periods of the day. A female, on the other hand, appears to gain in aggressiveness toward the end of incubation and remains quite aggressive at least until the young have fledged, and probably longer. In some cases she may become more aggressive than her mate. The female appears to "own" the nest and will drive birds of any species away from its immediate vicinity. This aggressiveness even extends toward the male, should he venture too close to the nest. I am almost certain that one female I watched succeeded in driving her mate away permanently once she began feeding the nestlings, an example of extreme individual variation. The tendency of the male to show interest in the nest, and the attentiveness with which he guards, are also subject to considerable individual variation. Once the eggs have hatched, both adults are active in defense. The defended territory, however, still remains an ill defined and variable zone, centering on the nest.

Observations by Davis (1941) on life history and aggressive activities of *T. tyrannus* differ in many respects from my observations. The reasons for this are probably twofold: (1) individual kingbirds differ markedly among themselves in what might be called "temperament," and (2) the same individual may react very differently at different times to situations that appear very similar to the observer. The fact that I have watched a much greater number of individuals and have had the benefit of a greater total amount of observation than had Davis probably accounts for most of our differences. On the whole I find only that most of his restrictive statements are too narrow (e.g., females *will* at times attack non-predaceous species like House Wrens (*Troglodytes aedon*) that come close to the nest, and *both* sexes may reveal the concealed crown patch in aggressive encounters with non-conspecifics).

In the following presentation 19 displays are recognized in the repertoire of *T. tyrannus,* although some of them are of dubious distinction and have been treated as separate entities primarily to facilitate description, discussion, and comparison with other species in this and other genera. There are seven vocal displays, usually referred to hereafter as "vocalizations." Most of them are quite high-pitched. These are: Locomotory Hesitance Complex of Vocalizations, Incipient Locomotory Hesitance Vocalization, Repeated Vocalization, Attackee Vocalization, Chatter Vocalization, Compound Vocalization, and Regularly Repeated Vocalization. Throughout most of the text they will be referred to by their initials (e.g., RRV). There are seven postures or movements used as displays: Wing Flutter, Tail Quiver, Wing Flick, Tail Flick, Crouch, Tumble Flight, and Gape. There are two non-vocal sound displays: Wing Whirr and Bill Snap, and three recognized plumage erection displays: Revealed Crown Patch, Raised Revealed Crown Patch, and Crown Ruffled.

Readers whose interests are not directly concerned with ethology or with zoosemiotics may find the following description of these 19 displays rather involved. I would suggest that the nature of the material under analysis can be sampled by reading about the first display, and that it should be possible to understand the discussion sections in Chapters 3, 9, 10, and 11 without studying in detail what is said about each and every display. Similarly, those who read the description of the displays of *T. tyrannus* may not wish to pursue the comparative material of Chapters 4–8, but to go on to the conclusions derived from these chapters, which appear in Chapter 9.

Chapter 2.

VOCALIZATIONS

Locomotory Hesitance Complex of Vocalizations

Description. The LHV of *T. tyrannus* is usually a fairly prolonged vocalization, comprising a series of repeated units. Each unit is complex, beginning with a brief, noisy burst in which frequency fluctuates rapidly over a large range (best visualized by reference to the illustrations of sonagrams), and followed by either a briefer, but similar, burst at a slightly lower average frequency (in which case the whole series definitely sounds harsh, see fig. 2:1b), or by one or two, rarely up to four, brief notes that lack the rapid frequency fluctuation (see fig. 2:1a; such a series is not noticeably harsh). The units sound something like "kt-ter", or "kt-ter-ter", and I have previously described this vocalization (1963 and 1965) as the Kitter display. I have stopped using this onomatopoetic name in favor of a more cumbersome one in order that homologous displays may share the designation in species where the sound may be quite different. No vocalization of any sympatric species sounds closely similar to the LHV of an Eastern Kingbird. Because it is prolonged and complex, it provides an excellent vocalization for a recipient to use in identifying the species.

Although all LHVs sound rather similar to the human ear, the amount of variation possible in a given LHV, or among various LHVs of the same individual, is remarkable. In addition to variations in obvious characteristics such as total length or loudness of the series, there are differences in the frequencies of successive "ter" elements, in the presence or absence of some of these elements in any given unit of a series, and in the degree of rapid frequency fluctuation of any element. Some of these variations have characteristic usages which I have identified, but others have yet to be pinned down. Further, the LHV forms intermediates with nearly every other vocalization of the species. Although such intermediates are relatively rare, they are potentially of considerable importance, and each will be discussed under each respective other vocalization.

Females very rarely utter this vocalization except during exchanges with their mates, with the result that it is very difficult to obtain a clear picture of the forms they employ. Typically, a female gives a shorter series than her mate, begins after he does, and stops before he does, so that the complex units of the calls of both birds overlap in a sonagram. If the male gives an unusually prolonged LHV the female may lengthen her series, or may repeat it once or twice while he calls. Extensive tape recording has shown that most LHVs of females are fairly similar in pattern to those of males (fig. 2:2a) although they seem even more variable, and are much more likely to contain some arched, high-pitched elements (described later in this chapter) if the male approaches closely or aggressively during an encounter between mates. In such instances the males customarily use the harsh form of the LHV; at least occasionally, females reply in kind, although usually at a slightly lower frequency.

Use. Within a breeding pair LHVs are frequently uttered by one or both individuals when one approaches the other. When the kingbirds are unusually agitated, almost any movement by either individual may be followed by both birds using LHVs, but the most standard usage of the vocalization is when one bird rejoins its mate after an absence to forage or to collect nest material. Whether male or female calls first often depends upon which is more active at the time, but at least up through the period of incubation the male, who is then the more inclined to defense and aggressiveness, usually initiates the calling whether he is active or not. When mates approach each other in flight, particularly if they are for any reason agitated, one or both is likely to use the LHV. Should a male suddenly turn on his mate while giving a harsh form of this vocalization, he may briefly attack her, although she is not likely to fight back. These attacks are relatively rare, and probably occur most commonly during the period of nest building, when the guarding male often flies out to meet his mate as she returns with nest materials.

In use of the LHV within the pair both individuals show a customary orientation. They rarely face directly, but usually align so as to point past one another. Thus, if they are perched on the same branch they may face in opposite directions or in the same direction, as long as they are so oriented that their sides are toward one another. In most cases these relative positions will be maintained through the vocalization, and the birds will settle down quietly near one another without further interaction. On the other hand, they will not usually settle quietly if one breaks the orientation and faces the other. Nor is use of the LHV with proper orientation always followed by peaceful settling. For instance, I have known females to use the LHV when repulsing copulation attempts by their mates, and there was often further interaction after its usage. Also, when one or the other individual is particularly excited, use of this vocalization does not always preclude the possibility of a short fight. While such fights are seen fairly often early in the breeding season, they are rare relative to the total number of interactions between mates which use the LHV, and it is safe to say that the use of this vocalization within the pair customarily is followed by a period with no further interaction. Sometimes the characteristic orientation will be interfered with without causing any disruption of intra-pair behavior. I have, for instance, watched a male who would customarily give the vocalization from his guard perch each time his mate returned to work on the nest, but who steadfastly kept facing me — even when this meant he had his back toward his approaching mate.

During the period of pair formation, nest site selection, and nest building, the LHV is used very often, and two birds calling it in flight, as one (usually the male) follows the other, is common. During the period of incubation the pair members seem to have become accustomed to one another, and they use the LHV much less frequently, often not even when disturbed. Once the young hatch, however, the adults, particularly the female in most cases, become more and more aggressive, and the LHV once more becomes common. This is most easily seen when an observer approaches a nest. He will be harassed by both adults making swooping attacks on him, calling the LHV each time they swing past one another. (The LHV may also be used when a harassing individual is making a wide, indecisive appearing swing away from the intruder instead of attacking.) Finally, by the time the young are at least ten days fledged the call begins to be used by all members of the family, and a fledgling will often use it while following a parent to beg.

This same vocalization is used, although not extensively, by male Eastern Kingbirds during stalemate phases of territorial fights. In all such cases other vocalizations and postural displays are much more common than is the LHV, but either of two disputing birds may use it, and its indirect orientation remains characteristic. Interestingly, the frequency of usage may increase if one or both of the mates of the disputing males comes to the general area and watches the encounter, and either male may also turn occasionally toward his mate and exchange an LHV with her. Sometimes a Kingbird will give the LHV when inhibited from attacking, as when one flies up toward a larger bird such as a Robin (*Turdus migratorius*), stops short, makes intention movements toward the larger bird, and calls. The LHV may also follow fights or chases when the aggressor is returning to his perch. I once heard a male call it after chasing a Pigeon Hawk (*Falco columbarius*) which flew over his territory; it was not the call he used in pursuit, but the one he gave as his flight slowed and he began to turn to come back.

While the LHV is used extensively in encounters between birds, it is also often used by lone males when they are not close to any other member of their species. Before the onset of incubation, and to a lesser extent again after the young are fledged, a male will often spend prolonged periods throughout the day flying from tree to tree in his territory, using this and other vocal displays repeatedly. Bouts of such activity, which I find convenient to refer to as "patrolling," often build up in the absence of any obvious environmental changes, although they are also easily touched off by the sight or sound of another conspecific male behaving in the same manner. The different vocalizations are by no means randomly scattered through such a bout. The LHV (usually not the harsh forms) is most often used while the bird is approaching a perch, and sometimes on landing or (more rarely) immediately afterward. If a flight takes him close past several perches, he is quite likely to veer toward one of these, slow his flight and begin a landing approach, give the vocalization, then change and continue his flight, beginning the sequence over again as he veers toward yet another perch. He is not likely to settle long when he does land, but will usually give a few vocalizations and set off again for another flight of 30 feet or so. Most of the calls given from a perch are not LHV, and the few which are uttered are usually accompanied by flight intention movements. In these circumstances it is clear that the LHV is associated with a period of "indecision" in flight when a choice of continuing to fly or taking a perch comes up, and is also associated with a similar kind of indecision over flying or not flying once the bird has landed.

The correlation of use of the LHV with a situation in which the calling individual is motivated to fly, to continue to fly, or at least to locomote in some fashion, but is also for some reason hesitant to do so, is usually obvious. Relatively quite rarely, though, the LHV is given by a bird which is perched, which remains perched, and which does not perform any flight intention movements. In most cases this bird is a male who is at the same time using extensive Compound Vocalization, and there is reason to believe (see below) that the same indecision likely holds. Rarely, a bird which has been perched quietly for some time may give an LHV, without the usual posture or accompanying display movements, and continue to remain perched quietly.

Although patrolling is a prominent feature of the behavior of this species from the time males arrive in the spring until they are paired, or even until their mates begin to set, it becomes much less frequent subsequently. It does not by any means disappear, however, especially in localities where the species has a relatively dense population. Throughout the spring and summer there are two times of day when males are likely to be hyperactive and to do at least some patrolling. The most noticeable of these is early morning at about the time of sunrise; a less pronounced, and less regularly occurring period of activity comes at about sunset before the birds go to roost. In both of these crepuscular periods a prolonged and increasingly augmented bout of vocalizing is likely to lead up through one or more LHVs to a Tumble Flight display (q.v.). On one occasion I observed a period of hyperactive daytime patrolling by a male which lasted for several days after a predator had taken the nestlings of the pair.

Associated Displays. An LHV by a perched bird is almost always accompanied by the Wing Flutter, except in those very rare cases of a wholly inactive, lone individual who remains inactive even after calling. (These cases are so rare as to be almost certainly unimportant — it is as if an otherwise quiescent bird suddenly had a burst of motivation which, in some sense, "surfaced" but which was only instantaneous.) In addition, a calling bird always pulls back its head, ruffles its crown feathers, and usually spreads its tail; it may also quiver the tail, a small amplitude motion impossible to detect at any great distance. The same body positions and movements (except possibly the tail quivering, about which I have no information) accompany the LHV during flight (discussed under the Wing Flutter display), although in very rare instances a lone individual may give an LHV in flight with no accompaniment.

Message and Meanings. The functioning of the LHV is best understood within the framework of the whole set of signals used by the species, and will be treated in the discussion section. At this stage, though, it is possible to state the apparent message of the vocalization, and this, paraphrased, would seem to be "I, an Eastern Kingbird, am experiencing some conflict with a tendency to locomote." In most, but not necessarily all cases, the locomotory tendency would be one of approach. This simple message is placed in a wide variety of contexts, and must generate a large number of meanings.

Within the pair, the most useful and most likely simple meaning to the recipient results from the probability that the communicator is not likely to approach close enough to attack (in part probably because it recognizes its mate), so that the recipient of the signal need not flee or defend itself. (Harsher forms of the LHV, however, encode progressively greater probabilities that an aggressive tendency may come to predominate in the communicator). If the communicator is already approaching while calling it seems likely that in many instances aggression is not a major part of the motivation, although the message does not make clear what sort(s) of motivation may be responsible for the approach. If a bird is perched while LHV calling (as, say, a female in repulsing a copulation attempt by her mate), it may mean to the recipient that the communicator will permit no interaction other than approach, but will not likely attack or flee.

The display may also be used by males engaged in a (stalemated) fight. Here neither attack nor escape is immediately likely; for one reason or another, the communicator is inhibited from advancing or retreating.

Uttered by a following bird, the meaning of the LHV will depend on the context of the following. For instance, a male following his mate and calling the LHV will make available to her the meaning that his following is inhibited to the extent that it is not likely to become aggressive or sexual pursuit. When fledglings follow their parents, they could easily be mistaken for neighboring adults who might be attacking; the parent receiving an LHV in such a situation obtains the information that (a) the following bird is not about to attack, and (b) the communicator is probably one of its own demanding offspring.

In daytime patrolling a male utters the LHV while alone. The display in this context must indicate first that the communicator is so restless and indecisive as to be constantly flying and pausing. This in turn, early in the spring, can indicate to a migrating female that the communicator may be an unmated male, since only males patrol, and since the frequency of such patrolling activity falls off at or before the stage of incubation. To a migrating male it can indicate that there is a conspecific male already settled and defending territory in the area from which the calls are heard. A female may also at times use the LHV while alone as she flies from her nest to forage in the absence of her mate and is hesitant about leaving. To the recipient mate this use of the LHV must mean that the nest is now unguarded and that he should fly to a guard perch.

Incipient Locomotory Hesitance Vocalization

Description. The ILHV is a two part vocalization, closely related in form to non-harsh LHVs. The first brief burst fluctuates rapidly in frequency and is closely similar to a slightly or considerably lower pitched first element of an LHV. This is followed by a clear sounding, simple, descending element (fig. 2:2b) longer than the sum of two of the final elements in an LHV unit. In fact, where several ILHVs precede or follow an LHV this simple descending element may appear to become lower pitched and break apart to form the related elements of the LHV, or it may appear to develop in a number of stages through the coalescing of such LHV elements. To the human ear this vocalization is a brief and almost explosive, high-pitched "kt-zee" or "t-zee."

Of the detected variations in this vocalization, most seem to occur in the "zee" element. The initial element varies somewhat in length (though always brief), in the abruptness with which it terminates, or in the manner in which it bridges the gap to the second element, but these variations are not yet well understood. It is quite possible that they are too brief, or otherwise too difficult to detect, to be of any communicative significance. On the other hand, it is clear that at least some of the modifications of the "zee" element considerably change the sound of the call. The least noticeable of these variations occur in the initial segment of this element (see fig. 2:2c) and most commonly appear as a brief, abrupt jump to a parallel bar (as it appears on a sonagram) higher than the usual pattern of the "zee", followed by an equally abrupt return to the usual pattern. More rarely this short higher bar is produced without the main form of the "zee" being broken, and two or three similar bars appear below the "zee," spaced at regular intervals. (This is helpful for analysis, as it suggests that the bird is producing the modification by selecting, from a set of possible resonance harmonics, one or more which are not usually emphasized.) A more spectacular variation, and one which is clearly detectable by the human ear, involves an arching and emphasis of the "zee" element, giving the impression of higher pitch. This form intergrades with a not wholly distinct vocalization which I describe later in this chapter as the Attackee Vocalization.

Use. ILHV is not a particularly common vocalization. Unlike the LHV it has no customary postural or display accompaniments, and it often bears no obvious relationship to a tendency to fly. It is much more likely to be used by a perched bird without flight intention movements than is the LHV. In fact, it seems as if it might be a vocalization which replaces the LHV at relatively low intensities of the conflicting tendencies which appear to underlie the longer call, and yet is given only by fairly agitated birds. When the ILHV is given in flight it may be repeated several times either before or after an LHV. Quite rarely, a rapid series of ILHVs may be used on approaching a perch, typically by a bird that has not been vocalizing extensively. Such a series of ILHVs may also precede the LHV of a bird approaching its mate; even more rarely they may replace the LHV under these circumstances, and are then sometimes accompanied by an abbreviated, jerking, Wing Flutter.

In other situations where this vocalization is used there is apparently an element of fear governing the bird's behavior. This can easily be seen by placing a stuffed owl near the nest tree. The male kingbird will usually approach and attack the mount at least a few times, calling some variation of the ILHV as he swoops upward from each diving attack. It is in such cases that I have recorded variation in the selection of resonance harmonics in the first part of the "zee" element. He is also likely to perch nearby where he can watch the mount, and repeat the ILHV rather frequently. In a more natural situation, the vocalization begins to be given as he starts to slow down while chasing a hawk. Females also use the call when faced with a potential predator near the nest; I have had them perch near a nest and peer nervously at me, calling the ILHV. I have also seen a guarding male on a telephone wire supplanted by a Mockingbird (*Mimus polyglottos*) move down the wire a few feet, perch again, and then utter several ILHVs over a period of less than a minute.

Message and Meanings. The message appears to be a low-intensity version of the LHV message: "I, an Eastern Kingbird, am experiencing some interference with a tendency to locomote." (The locomotory tendency, the interference, or both may be weak.) The ILHV can thus also have meanings similar to low intensity versions of the LHV meanings, but it seems to occur more often when an element of danger is present, and in such cases the meanings shift, adding the implication that the communicator is defensive and inhibited from aggression.

Repeated Vocalization

Description. The RV is a vocalization comprising only one element; it is marked by a rapid and extensive fluctuation in frequency which gives it, at least to human ears, a harsh quality. It usually sounds to me like "zeer". Several forms are shown in fig. 2:3a and d. The call may be relatively "flat" or moderately to strongly arched; sometimes it begins with a very abrupt front; sometimes it is shortened markedly, and sounds more like "tzit". It varies markedly in the range of frequencies spanned by its fluctuations, and sometimes this range will double or halve during a single "zeer". The RV intergrades in various ways with the ILHV (see fig. 2:2d), and, when given in series of couplets in which the second element is briefer and peaks at a lower frequency, it becomes the harsh LHV. As such, it also apparently intergrades with the Chatter Vocalization (described later).

The harshest sounding form of the RV is probably not species specific, but convergent with calls used in similar circumstances by many other species. The commonly repeated forms are more species specific.

Use. The RV is much more commonly used than the ILHV or even the LHV; at any particular time of day it is the call most likely to be heard. It is given occasionally or frequently by a male on one of his guard stations who appears to be in a guarding mood. The form used is variable, even for any one male within any one hour, but it is almost always one of the longer possibilities, either arched or moderately flat. A male who is flycatching or resting, or who is far from the nest tree, does not usually call. One that has stopped on the nest tree, or on some tree within 50 yards or so, may utter a single "zeer" every few minutes if preening or if apparently alert. His rate of calling may vary considerably, but when it reaches one call every two to five seconds, he is particularly likely to change perches or even to attack intruding birds he would not otherwise attack — i.e., species smaller than himself, or birds passing at a sufficient distance from the nest to be usually tolerated. (Hawks and other large potential predators are usually attacked on sight anywhere in or near the territory by even the most phlegmatic appearing individuals.) Rarely, an individual who appears to be alert but who is *not* calling at all will engage in more than the usual amount of chasing of passing Starlings (*Sturnus vulgaris*), Common Grackles (*Quiscalus quiscula*), and other birds, but this is clearly exceptional. Timing intervals between utterances of this call by guarding males has shown no simple relationship between rate of repetition of the RV and likelihood of flight (including foraging flights), but tends to support a generally greater probability of flight when calls are frequent or increasing in rate.

The RV is also very common in patrolling, in which a considerable part of its usage is in an apparently ritualized combination with the Chatter Vocalization, and will be discussed later. Part of the remainder of its usage in patrolling is an irregular repetition of up to one call every two to five seconds, and is identical with the calling of a guarding male. Strings of rapidly repeated RVs often precede LHVs during patrolling, in much the same fashion as the ILHV may. At some such times the distribution of sound energy within the call varies sequentially and results in forms not unlike some of the variations of the ILHV, making it a harsh sounding substitute for that vocalization. LHVs that follow such strings are often themselves harsh, and formed of units with only two elements (as in fig. 2:1b).

At least males give an occasional RV most nights after going to their roost sites, calling intermittently in the last minutes of the fading twilight.

An Eastern Kingbird which is about to attack or is attacking uses a harsher version of the RV almost exclusively. (In some species where the RV is not harsh I have distinguished harsh calls used in attack as Attack Vocalizations, AtV; in *T. tyrannus* where I should find it difficult to distinguish RV and AtV I have made no formal distinction. This has been an arbitrary decision, and perhaps in the future it will be better to recognize an AtV in this species.) There may be a quick succession of intermediates from a more-or-less standard form of the RV to an extremely harsh form in which the magnitude of frequency fluctuation is greatly increased (see fig. 2:3d). The harshest form, often abbreviated, usually comes just as the bird is about to strike, or is actually striking, or is at least at its closest point of approach to the object of its attack. (Observations of birds attacking me, and experiments with a stuffed owl show that the attacking bird often pulls up just short of its target; one does see contact made, however, and sometimes a kingbird will actually grasp the back of some large, slow-moving hawk like a *Buteo* and hold on, pulling out feathers with its beak). Males may attack anywhere within or near their territories, but will attack most readily near the nest tree, while females attack only in the vicinity of the nest or young. Both parents attack most vigorously when there are young in the nest or recently fledged. Almost any potential predator may be the victim, from approaching humans or cats to avian predators and non-predaceous birds like gulls and thrushes down to kingbird size and sometimes smaller. The last are often driven away with little or no display, perhaps just a Bill Snap or some feather ruffling, but all others normally elicit the harsher RVs and sometimes repetitive strings of less harsh RVs between attacks. All forms of the RV are common in fights between neighboring territorial males.

As a rule, whenever a kingbird sees a passing hawk it begins to call the RV, then proceeds to attack, or at least to chase or follow. Dangerous hawks like accipiters or falcons are not usually (in my experience) approached closely. During chasing or following, the kingbird is likely to stop using the RV and begin using the ILHV, perhaps passing through some intermediates. In experiments with a stuffed owl it was clear that the RV was uttered in and immediately before swooping on the decoy; it might also be used by a bird hovering between swoops, in which case a brief span without frequency fluctuation — like the "zee" element of the ILHV — sometimes appeared within it. The ILHV was used on pulling up from a swoop, or between swoops, and showed two sorts of variation. One, the addition of brief supernumerary bars harmonically related to each other and to the "zee" element has been mentioned previously. In the other, a form intermediate between ILHV and RV, the "zee" element would show a few or many areas of rapid frequency fluctuation in its mid-part, or would terminate in a pronounced burst of such fluctuation (example in fig. 2:2d). This particular sort of variation can apparently be produced by the modification of either an RV or an ILHV.

Much as it switches from the RV to the ILHV in most instances of pursuing, a kingbird will switch to the higher pitched ILHV (or even to the Attackee Vocalization, see below) during an encounter if it loses the advantage. This may occur if it attacks a bird larger than itself, as a Blue Jay (*Cyanocitta cristata*), which it can sometimes defeat, and sometimes not; or more maneuverable, as a Tree Swallow (*Iridoprocne bicolor*), which can almost always gain the advantage alone, or very rapidly in a flock. Further, there are instances of behavior that are not properly attack but that may lead to use of the RV. This sometimes happens when a kingbird is pursuing a large and elusive insect through a number of sharp turns and evasions without success; the bird may finally begin to give a few harsh RVs as it darts about. Once such activity brought a kingbird progressively closer to me, and when it began to call it used the ILHV. Finally, there have been cases where a male kingbird was not attacking me, but facing me and calling the RV as I stood not far from the nest. When the bird's mate approached, he sometimes turned toward her and changed his call to the ILHV.

Message and Meanings. The RV in its harsher forms seems to signify an aggressive mood in the caller. On the other hand, use of the less harsh forms of the vocalization during guarding does not necessarily indicate that the bird is aggressive at the time; these less harsh forms probably do indicate that a relatively slight change in the environment is more likely to influence him in the direction of increased aggression than it would if he were not calling the RV. They also identify the species. The message may be modifiable (with increasing harshness of the call) from a defensive to an offensive statement, the latter indicating aggression, the former only latent aggression. In addition, though, the message seems to overlap with the message of the ILHV, that a tendency to locomote is present but either being interfered with or not yet well developed (which may also be due to interference).

The significance of the RV varies from being straightforward (the caller is attacking or likely to attack) to indirect (the patrolling or guarding caller is a territory holding male Eastern Kingbird who can easily become aggressive) as different contexts are considered. A particularly interesting possibility, but only a possibility at this stage of the research, is that an incubating female may learn from the call that her mate is in a guarding mood at times when she cannot ascertain this by watching him.

ATTACKEE VOCALIZATION

Description. The Attackee Vocalization sounds like a very high-pitched, rapidly uttered "tee" (fig. 2:3b), usually repeated about three to five times. The form is like a highly modified "zee" unit from an ILHV, and it forms intermediates with that vocalization and with the units of the LHV, (see fig. 2:2a), and perhaps with the RV. Possibly the AeV is just an extreme modification of the ILHV, but the intermediates are all irregular patterns given at times of abrupt change, and some uses of it are fixed. It is therefore more convenient to classify it as a distinct vocalization.

Use. When two kingbirds are engaged in a grappling, wing-banging, biting, aerial fight with each other, both are likely to call the very harsh forms of the RV in the early part of the fight. Should one gain the advantage, however, it will continue this call while the other switches, sometimes through an intermediate (or an RV/ILHV intermediate; it is hard to tell) to the Attackee Vocalization, shortly before giving up the fight and fleeing. A Kingbird that attacks a larger bird (like a Robin) and loses the initiative will usually switch from the harsh RV to the high AeV, although sometimes just to the ILHV. A bird losing an attack to some smaller species, as a Tree Swallow will switch simply to the ILHV.

Sometimes a high "tee" call is used by an Eastern Kingbird that is being attacked by, attacking, or even chasing some similar sized or larger species such as a Cedar Waxwing (*Bombycilla cedrorum*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), or Baltimore Oriole (*Icterus galbula*). Such instances usually happen very suddenly and are very brief; in most cases I am not sure I saw all that occurred. In only one case did I see the entire event *and* obtain a recording. This involved a male kingbird who took a perch very near a Baltimore Oriole nest; within a few seconds he was attacked by the returning female oriole, fought or faced her for less than a second, then fled.

She flew toward him with a harsh, repetitive call (probably the oriole equivalent of a harsh LHV), then attacked with a series of harsher, more prolonged calls. At the point where she switched from one type of call to the other he uttered an intermediate ILHV/first unit of an LHV, and one-half second later gave a single "zee" or "tee" unit. This was shaped like a standard "zee" from an ILHV but peaked nearly 1 kc. lower, although fully 1.25 kc. higher than the "zee" element of his preceding call. It was not an ILHV (it lacked the initial harsh element) and not an AeV (it was too simple — see fig. 2:3c) but was one of the possible sorts of intermediates between them. Almost certainly it was the same as other calls that have sounded to me like high "tee," and this further strengthens the case for considering the ILHV and AeV quite closely related. This high "tee" can be uttered by either sex — at least once I am sure that a kingbird using it in an attack on another species was a female.

The AeV is the vocalization most commonly used in the tumbling portion of the Tumble Flight display, a highly stylized behavior described in detail in Chapter 3. Finally, a similarly high pitched but longer element making up the terminal portion of the RRV (described below) resembles the AeV closely.

One variation of the AeV is almost characteristic of females. At some nests a male will often fly out from a guard perch to greet his returning mate with a quite prolonged LHV, to which she usually gives a much briefer reply. On occasion he may swing very close to her back and even attack her, and she will then give a brief LHV that ends with a unit or units intermediate to the AeV, or give a brief LHV made up entirely of such intermediates. She does not fight back, and she does not flee — she flies on to her nest.

Message and Meanings. If this vocalization occurred only in fights, its message would likely be one indicating fear. Its occurrence in the Tumble Flight display makes this too restrictive an interpretation, however. It is as if the vocalization were sometimes dependent upon the motivation of fear and sometimes emancipated from it. The best message interpretation may be "I, an Eastern Kingbird, am a frustrated fighter," inasmuch as the bird gives the vocalization while still fighting, although only when losing the fight, or when being attacked but not fighting, or, in the case of the Tumble Flight, when fighting as if "in vacuo." In context it may indicate that the bird is likely to cease fighting and flee, and that the aggressor can cease fighting. In the case of the Tumble Flight (q.v.) it indicates that the bird is a male Eastern Kingbird in a mood to defend his territory.

CHATTER VOCALIZATION

Description. A CV comprises a rapid or very rapid series of simple, brief elements. Each element is sharply chevron-shaped on a sonagram (fig. 2:4a) and has a duration of only about 0.01 to 0.02 seconds. In extended series 20 to 25 or more elements recur per second. Within a series of any length there is often a regular fluctuation of frequency and amplitude, and in prolonged series this fluctuation usually takes a sinusoidal form.

Males commonly give related brief series terminating in a single RV, the whole being repeated as a unit. This form is so standardized that it will be treated below as a distinct display.

Other variations occur frequently. A series can be hesitant-sounding, with pauses and with relatively few elements per second. Such cases are commonly composed of pairs of elements in couplets (fig. 2:4b) in which the first element usually peaks at a lower frequency than the second, the converse of the arrangement of similar appearing elements in the unit of a standard LHV. Couplets are likely to occur whenever "hesitation" occurs within the delivery of a prolonged series, and sometimes come at the start or end of a series. A CV series can also be harsh, and the harshest can intergrade with the harsh form of the LHV or with the abbreviated form of the RV. Such harsh CVs, in fact, usually have obvious affinities with either the LHV or the CdV, and need not be considered here.

Use. The CV is much more characteristic of females than of males. It is rarely used away from the nest site, and is heard often while females are building nests. A faint-sounding CV is usually uttered by the female when her mate appears close to the nest, or when an observer stands sufficiently close to attract attention without being close enough to cause overt alarm. A building female slightly more disturbed by the presence of an observer will cease work, face the observer, and use this call; one such female looked alternately at me and at the nest, while maintaining a loud, rapid, very prolonged and high-pitched CV. Often the mate will come when the female calls and will perch nearby, but I have never seen a male Eastern Kingbird attack or even approach close enough for any contact with a female that was using the CV at a nest. Males who occasionally guard too close to the nest (some will stand on the nest rim at times) will usually elicit this call from a mate returning to incubate, or even a mate leaving the nest to forage. A female returning in such a case will give the call harshly and may strike her mate, but more often she will simply supplant him. The harsh CV is probably indistinguishable from a short series of abbreviated RV notes (described above as "tzit"). If a female is incubating or brooding when her mate returns from one of his foraging absences and lands on a perch within a few feet of the nest, she will often give this call, usually in a high form, and remain on the nest. In fact, when a female uses the CV she is most often in a nest or nest site, either setting, brooding, prospecting, or building, and she usually persists in her position.

Males use the Chatter Vocalization relatively rarely, except, perhaps, during the early part of the season before the females build. At that time there is the behavior pattern which appears to be a showing of potential nest sites by a male to a female. When so occupied, a male utters prolonged strings of pure CV in a form quite indistinguishable from that used by females when they are nest site prospecting, or when they are working on a nest.

I have rarely heard a male use the CV when with his mate (who was also calling it) in the vicinity of the nest or young fledglings where they were disturbed by some such cause as my presence nearby. I have also known only one male who fairly persistently came from a guard perch over the nest to stand on the nest rim and peer in at the eggs during his mate's absences. He often called the RV and the CdV (described below) while there, and very occasionally gave a faint CV. Sometimes a pair will cease using the LHV with WFt when meeting at or near the nest or nest tree late in the period of incubation. When they do greet in such circumstances, the female will utter a CV and the male a CV with occasional RVs interspersed (i.e., an irregular CdV); neither will give a good Wing Flutter, but the male, at least, may partially lift the wings away from the body. Even before this stage of apparent familiarity is reached, some females respond to LHV with WFt greetings by their guarding mates only by calling a CV as they settle on the nest.

The couplet form variation of the CV often seems to be given by a bird that is more disturbed and more active than would be a bird that gave a faint, prolonged CV. It sometimes, but not always, leads to use of the prolonged call.

Sometimes a very harsh (for this vocalization) and loud form of the CV apparently intergrades completely with the harsh LHV. It is used within the pair by either individual during a mutual approach when both are aggressive (as when a male has been swooping at a stuffed owl and is joined 100 feet or more back from the decoy, by his mate). I have once known it to be used early in the season by a female, who also used definite LHVs, in repulsing a copulation attempt by her mate.

Message and Meanings. Although the female usually gives the CV from the nest, or from at least near the nest or fledglings, she may be doing any one of a number of things and is not likely to switch to some other behavior pattern when she calls. This suggests that the message is one of general anxiety over a situation in which the nest (or young) are important. This could even be the message when no nest yet exists, and she is trying to pick a site for it; probably no site suits her immediately, and perhaps none is perfect. At times the male himself may well be the cause of her anxiety, since he is likely to interfere with her activities. It is much more difficult to see a message in the male's use of the vocalization, but it is *conceivably* the same message.

For the female's uses a single interpretation is likely: that the communicator is aware of a problem concerning the nest, nest site, or young, perhaps of a potential danger to these, but has not yet resolved the situation and may not cease her present behavior. The call gives no indication of what her reactions may be if the cause of her anxiety is resolved. This interpretation also fits the rarer uses of the CV by males, but the occurrence of the vocalization in what I believe to be nest site showing by males in a situation which is likely relevant to pair bonding must have quite different implications. If I have interpreted such situations correctly (and this remains to be shown by future research) then the display possibly indicates that the male is trying to form a pair bond with the recipient of the display, and/or is ready to copulate with her.

Harsh variants of the display may be misidentified. If such vocalizations do, in fact, relate closely to the CV, then their messages must indicate a much greater probability of switching from some action such as incubating or nest building to overt aggression. The messages may be modified to include the notion "will attack if pressed." This includes some of the locomotory hesitance message of the LHV, which may be why harsh CVs often appear intermediate to (or indistinguishable from) some harsh LHVs. Interpretation of such intermediates is perhaps best left to the discussion section later. It is worth noting, though, that females using the CV are almost never approached closely enough for contact by their mates, even though the latter seem to be attracted. It is possible that there is some element of "defensive threat" (term from Tinbergen, 1959, p. 25) in the message of any form of the CV.

Compound Vocalization

Description. This vocalization is essentially a CV terminating in an RV (see fig. 2:5a, c). Almost any form of either vocalization may be used, although certain combinations are more probable than others. Often the ultimate element of the CV is modified, and the series sounds as if it ends not in a "zeer" but a "t-zeer." These modifications may be either simple amplitude or pitch changes in the CV element, shifts in its position in time with respect to the rhythm of the CV series, or changes in a direction that makes it more like an exceptionally abbreviated RV unit. The couplet sort of CV is apparently more likely to have its last element modified than are CVs in which all the elements are closely similar, and the modification is usually like an RV fragment (see fig. 2:5b). Any length of CV from a single element to a prolonged series combines with an RV, but, while several RVs may follow a CdV, it apparently almost never happens that two or more are closely juxtaposed at the termination of a CV. The sinusoidal fluctuation of frequency and amplitude characteristic of most CVs is often maintained unbroken when CdVs are being repeated.

Use. In contrast to the CV, this is primarily a vocalization of the male. Early in the breeding season males do considerable patrolling using the LHV, RV, and CdV, the last primarily when perched. As has been mentioned previouly, this activity becomes less frequent at least by the time the male is mated and has a nest on his territory. It continues to occur in crepuscular periods and sporadically during the day. Should disaster befall the nest or mate, the male is likely to begin patrolling again, even as late in the season as the end of July. When the nest has been destroyed and the female has survived, she may accompany him, but she calls much less. There seems to be little regular pattern to patrolling; individual Eastern Kingbirds apparently do not restrict themselves to a few preferred "song posts" from which to give the CdV, although they do show preferences for certain trees and spend more time in these.

The length of the CdV varies immensely in such usage, at times dwindling to single couplets or even single CV elements widely separated from a series terminating in an RV. Birds calling rapidly but using quite prolonged sets often remain perched longer than birds using shorter CdV series and couplet variants, but I have yet to establish any clear correlation between amount of flying about and length of the Chatter portion of the call. There is some evidence that moderate repetition of short CdVs accompanies moderately active patrolling; in such cases the LHV may be omitted, and a landing bird may give no Wing Flutter (i.e., show no hesitancy) and may even call CdV as it lands.

Patrolling, if the population density is high enough, brings male kingbirds together for disputes over territorial limits (there seem to be no firmly held boundaries). The CdV is very common in such disputes, being used before and during the actual fighting, and at least by the aggressor in the chases that may follow. It may be used in the Crouch posture (see below) by both individuals in a squabble, and may sometimes be as common as the RV. Harsh variants usually predominate at such times. I have been able to elicit some use of the vocalization from a male by placing a stuffed Eastern Kingbird in a Crouch posture within his territory, but the model did not hold his attention very long.

Male kingbirds use this vocalization not only when chasing or confronting conspecific males, but toward potential predators as well. Again, it is not as common as the RV in such instances. In experiments with a stuffed owl, I have had an Eastern Kingbird call the CdV as he flew toward the decoy or when perched between attacks, but use only the RV and ILHV when in its immediate vicinity. This same male later directed a CdV + LHV toward his mate as she flew toward him over 100 feet back from the owl, and then used a harsh CV-LHV intermediate. In more natural situations I have known males to use it when chasing hawks, crows, and blackbirds, and in "mistaken" chases of birds, such as herons, which do not prey upon kingbirds. It has also been used toward me as I approached a nest, usually by the male, but sometimes a female has joined him in giving at least a few CdVs.

The CdV is in some ways closely related to the Regularly Repeated Vocalization, and, with it, serves in part as the "song" of the species (discussed later). At times repetition of the CdV may precede the RRV, or even take its place. CdV is much more commonly used after the RRV at about sun up, however, when there is usually considerable patrolling. The patrolling during the evening crepuscular period is often much less active, and a male will often perch for prolonged periods, frequently calling an RV or a brief CdV, occasionally building up into an LHV and eventually into a Tumble Flight. At any time of day, the CdV may precede a Tumble Flight. Occasionally it is given in the level flight portions of this display, and it very rarely is used as the vocalization during the stalls and tumbles.

Guarding is another behavior pattern in which males may use the CdV, although still less commonly than they use the RV. In the relatively rare cases in which males closely approach the nest and peer into it, however, the CdV becomes the commoner of the two calls. In ordinary, rather inactive guarding, the Chatter part of the CdV is likely to be reduced to a minimum, often of one to three elements. Only when a guarding male becomes unusually agitated does the CdV become common, and it may then completely replace the RV. This is likely to happen when a male is guarding, and his mate does not return to the nest for an unusually long time (say, ten minutes — it varies considerably). For reasons I cannot usually determine, a guarding male will sometimes begin to give this call very rapidly, take up perches in or very near the nest tree, shift about nervously and pivot on his perch, make frequent intention movements of flight, and call the LHV frequently (perched or in flight). He may fly to and from a perch near the nest fairly frequently. Usually the female is not present at such times. If she returns he may continue as before, may stop, or may fly to the region from which he customarily gives his RRV and continue there. This kind of activity and calling is rare; it may be most likely to happen at about the time the female begins to incubate, but it is not limited to that period. It is probably only an extreme manifestation of the agitated behavior of males near the end of an unusually long absence of a female from the nest. On the whole, CdV is more common than RV in patrolling, and the converse holds in guarding.

On a few occasions, I have known CdV to be used with the nest-site-showing behavior of a male. One morning a male called the RRV for only a short period, then went to another tree and began the site-showing behavior with a very rapid and high CV, sometimes ending in a high "tee" element. A few times a male, followed by a female, has given brief CdVs instead of CV while doing the site showing.

While the use of CdV by females is rare, they do, as mentioned above, sometimes join their mates in calling it toward an approaching observer. Sometimes a female will give the CdV on being flushed from her nest by an observer, or on leaving the nest in the presence of her mate (the observer being distant), but I have very few observations of either occurrence. Once I watched a fight between two males, which was also watched by their mates. After the encounter had reached a stalemate one of the females flew away, followed by her mate; she gave a CdV, he gave a CdV and LHV. The other pair followed suit, flying off in the opposite direction.

Message and Meanings. The message can be inferred to be that the communicator is anxious, and likely to become aggressive, over some situation concerning the nest or territory. As in the case of CV, it may most commonly indicate that some potential danger to the nest exists. When a male uses the CdV in patrolling, it takes the meanings of that context; this is a male in possession of a territory and ready to defend it. When used in fighting it probably indicates that the aggressor is not fully committed to the offensive, but is likely to become so instantly.

Regularly Repeated Vocalization

Description. An RRV comprises two phrases rapidly and regularly alternated: "tt-tt-tzeer, t-tt-tt-tzeer-t-zeetzeetzee." The first phrase, and at least the beginning of the second, vary from individual to individual, and, to a lesser degree, even in repetitions by the same individual. The ending of the second phrase sounds very high pitched, and, in fact, the final "zee" element ascends very steeply to a quite high frequency (about 9kc, see fig. 2:6). The length of the two phrases together is a little over two seconds; usually about 40 phrases are given per minute.

Use. Beginning in the pre-dawn darkness each territorial male calls almost continuously, rapidly alternating the two phrases, from one or a very few perches. The period of display lasts 15 to 25 minutes, extending into the twilight but usually ceasing or becoming very irregular by at least 10 to 15 minutes before sunrise. It starts later and may persist longer or be less regular on cloudy or foggy mornings. Calling is sometimes preceded by a Tumble Flight (despite the darkness) or by RV (which may also precede the Flight), and rarely by bits of CV or CdV. As a rule, no other vocalizations interrupt the period of RRV once begun, and the bird does not fly about. There seems to be no special pose, although the bill may sometimes point slightly downward, and the bird may hunch forward slightly.

The display is apparently infectious, and at Delta all males within earshot began shortly after the first one of the morning. If he preceded his calling with a Tumble Flight they likely would, too. In the period following this display each morning all birds usually became very active, and there was much patrolling and interaction. Several males might converge and continue to use the two phrases, although usually with less precise alternation. The vocalization is best heard in a dense population such as Delta's; the birds observed in the East often gave only irregular RRV. This was particularly true of the lone New Hampshire male who usually had no other Eastern Kingbird with which to countercall.

Males get restive again toward sunset, and move about calling RV frequently. They may also add a few CdV, and occasionally, before nest building was underway at Delta, I heard a mated male using both RRV phrases almost continuously for several minutes early in the evening twilight period. Alternation at such times is imperfect, with more use of the first phrase than of the ascending second one. Tumble Flights are also used in this vesper activity, and late in the season only RV and Tumble Flights are likely. Use of the RRV at any other time of day is *very* rare, and is almost never prolonged or regular. Occasionally, however, it is heard during a thundershower or after a thunderstorm. Once a flying bird called the final RRV phrase twice in mid-morning toward the end of a confusing encounter near the nest among four adults and nestlings of one pair; this is the only occasion on which I identified the RRV phrase from a flying bird.

The characteristic of regular alternation of the two phrases is the most salient feature of the display, despite the fact that early in the season and often by sunrise alternation may be imperfect. During nesting it is possible to listen to several males at once all alternating the two phrases with perfect regularity, minute after minute. I noticed little consistent individual variation at Delta, and less variation there than the New Hampshire male gave.

Vocalizations such as this are rather widespread in the Tyrannidae, and have been described in the literature for a number of species, usually under the more palatable, but not more accurate name of "dawn song." Various authors have presented descriptions of the RRV of *T. tyrannus* which would seem similar to the one above, for instance Mayer (1952), Bent (1942), Miller (see Bent), Hausman (1925), and Saunders (1935). Oddly, of these only Saunders drew attention to the alternation. Hausman's paper contains good descriptions of the other vocalizations, but it should be noted that his "kitter" probably equals my ILHV. He described each phrase of the RRV as beginning not with a CV but with three ILHVs. I have heard such a form only rarely, very early in the season, and am inclined to doubt that his case could be explained by geographical variation (especially as he was working in New Jersey, and Saunders' description is based on nearby Connecticut birds). I suspect he was referring to the occurrence of the CV elements in couplets.

Mrs. Mayer's paper is interesting in that she studied the RRV for 45 mornings from May until the departure of most of her birds in late August. The pre-dawn performances did not cease until only one adult male remained in the area, but although he then stayed alone for nearly two weeks, he no longer gave this vocalization. My New Hampshire male was "lone" to the extent that the next nearest male could rarely be heard (by me) from where he displayed. On some mornings during at least the time of incubation he gave no RRV. When he did call, he introduced fairly frequent aberrations; he might give a short CV between the two phrases, he once alternated RV and a fairly high ILHV for several minutes, he occasionally gave only phrase two, pausing where he would have given the first phrase, and occasionally he would introduce strings of phrase one toward the end of a morning's calling or use only phrase one throughout.

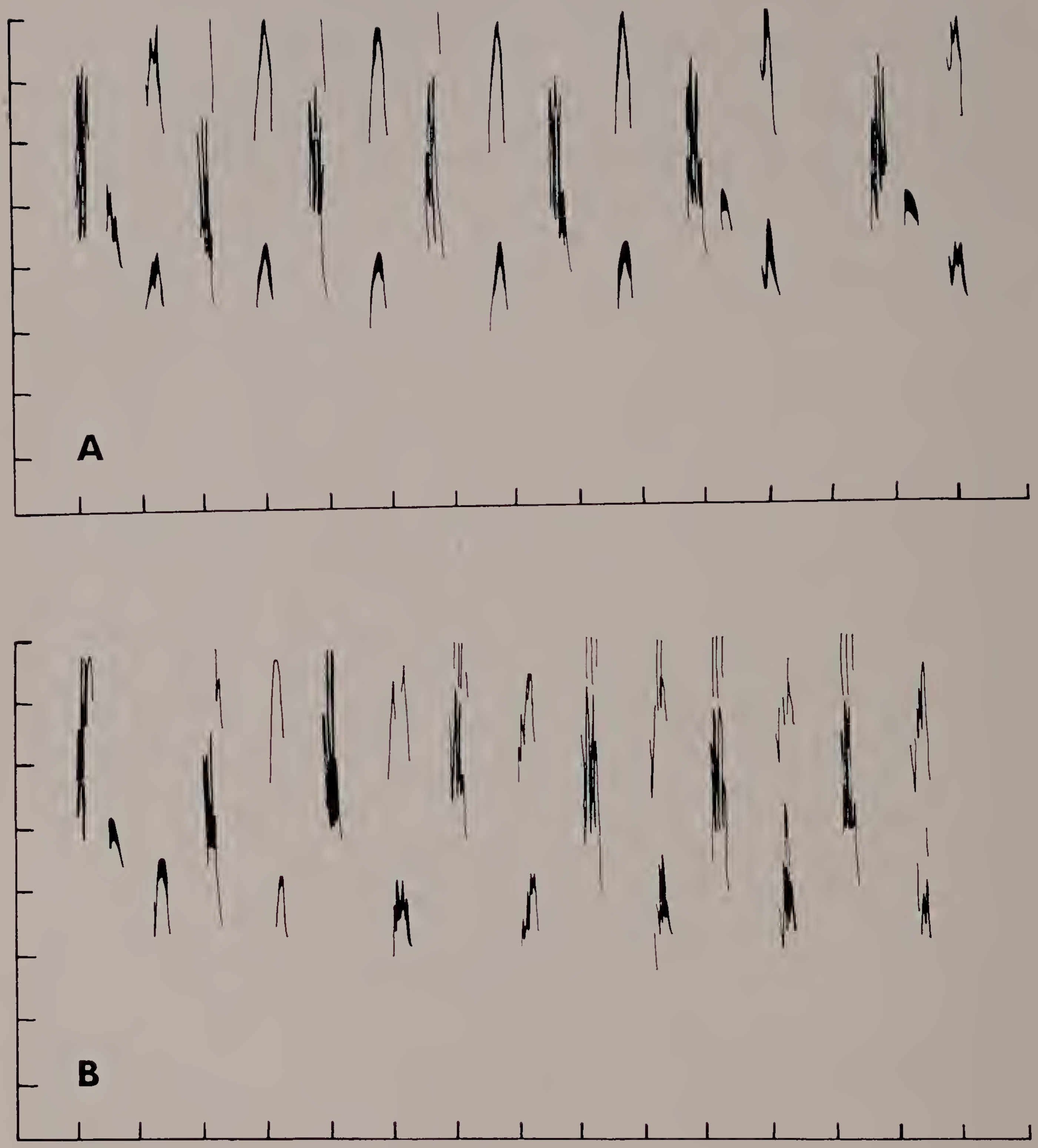
The RRV is followed by considerable use of CdV on most occasions, and it seems certain that this and phrase one are closely related vocalizations. Describing the CdV as closely similar to phrase one does not imply, however, that CdV is only a variation of the RRV since, after all, the alternating second phrase lends a considerably greater complexity to the latter vocalization. The CdV is not limited to use in the predawn twilight, and may serve as a less detailed replacement of the RRV; in form it is one sort of intermediate between the RRV and RV, and probably shares functions with both (discussed later). Perhaps significantly, one of the places a male may go to give the CdV when particularly agitated is the perch from which he gives his RRV.

On most occasions when I have been watching a RRV-calling male when his mate has flown to him, he has stopped calling. The Eastern Kingbird is not one of the tyrannids in which I have observed successful copulation, but in two cases in other species copulation occurred when a female joined her mate as he called the RRV homologue. In the other cases the male was not calling RRV when his mate flew to him, or he approached her. These limited observations permit few conclusions, other than that females are responsive to males when RRV calling, and may approach them and permit copulation. That males are responsive to hearing the RRV has already been mentioned; the display is infectious among males.

Message and Meanings. The RRV is the most complex vocalization of the species, and it can be remarkably invariant in some circumstances. The message is compound, and the display carries its information to unseen conspecifics, a task which probably requires the fixity of form and the prolonged period of delivery. Species identification and, probably (through consistent individual variants) individual identification are aspects of the message, as are sex (male) and breeding state (sexually active). Presumably it indicates a state of readiness to deal with territorial transgressors, as well as a state of frustration (it is given primarily when it is too dark to take any effective action, and the ultimate elements are closely similar to those of the AeV in which frustration seems likely).

The meanings to conspecific individuals depend on the sex of the recipient; a female may obtain the information that her mate is ready to copulate, another male may learn that his neighbor is still actively holding his territory. Perhaps only the last function persists through the season as late as August, for if females are uniformly unreceptive at that part of the breeding cycle, then their special contexts have been lost.

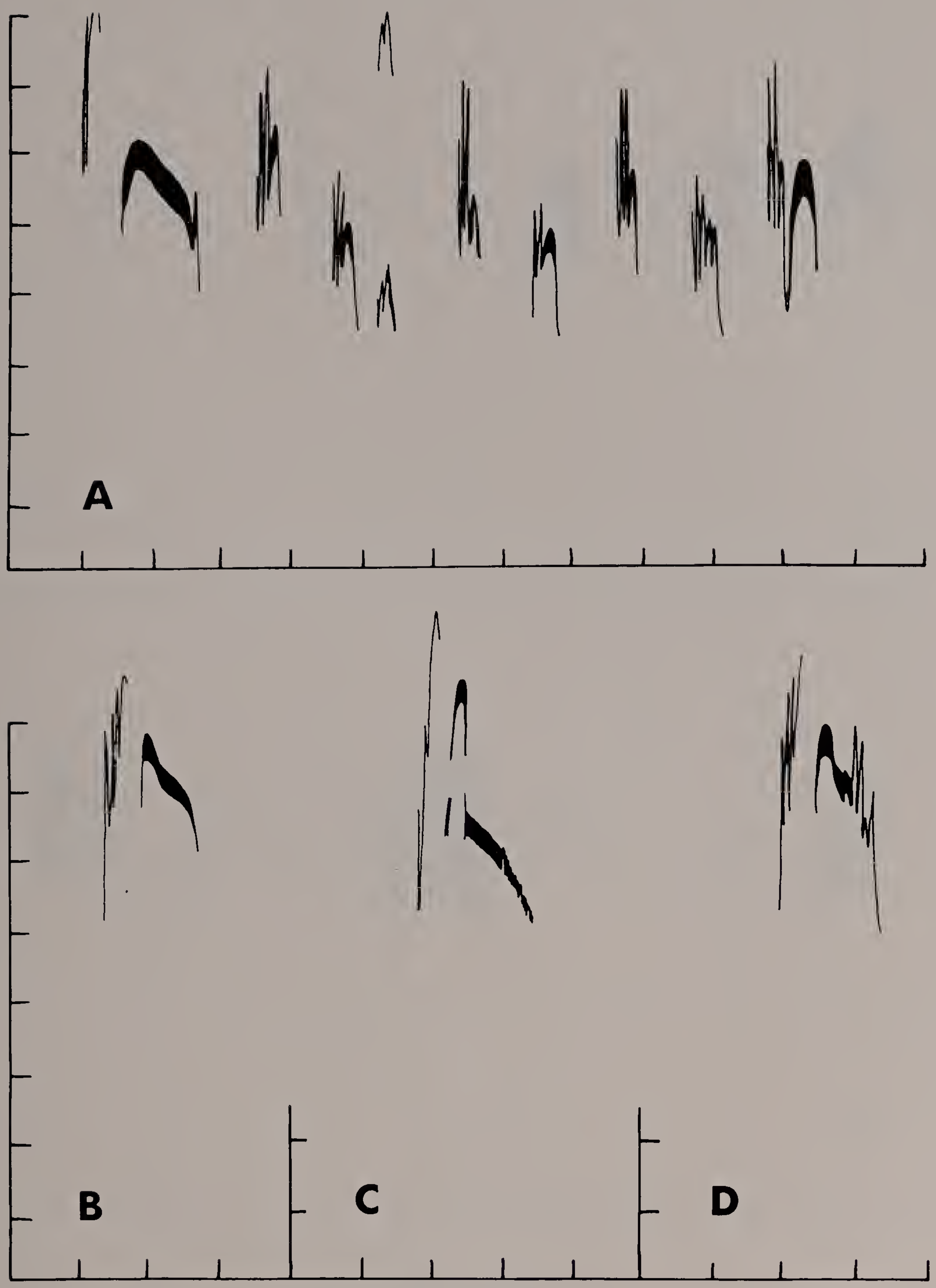
Figures



Tyrannus tyrannus

FIGURE 2:1a. LHV by a male immediately after landing, alone, by the nest. Note that it is just slightly harsh at the start, and the final element is slightly harsh. On this and all subsequent sonagrams, the vertical scale is graded in kilocycles per second (from 0 to 8 kc.), and the horizontal in 0.1 seconds.

2:1b. Harsh LHV by a guarding male as his mate flew from nest. Note that this example is not harsh at its onset.



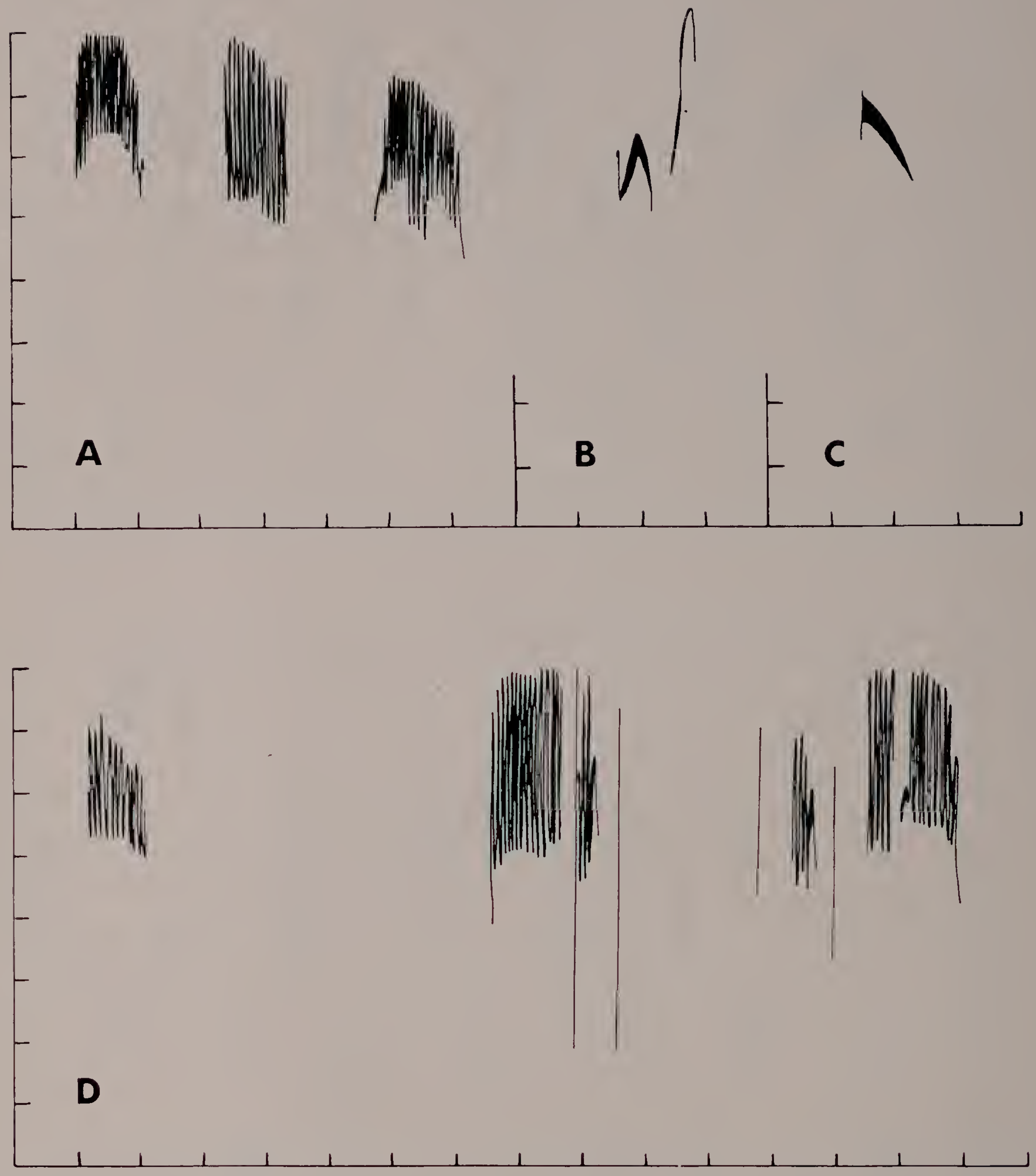
Tyrannus tyrannus

Figure 2:2a. LHV by a female greeting her mate as she flies from nest (his harsh LHV not shown). This is fairly harsh, and ends with an AeV-like unit.

2:2b. ILHV by a male flying several feet above a stuffed Little Owl after attacking it.

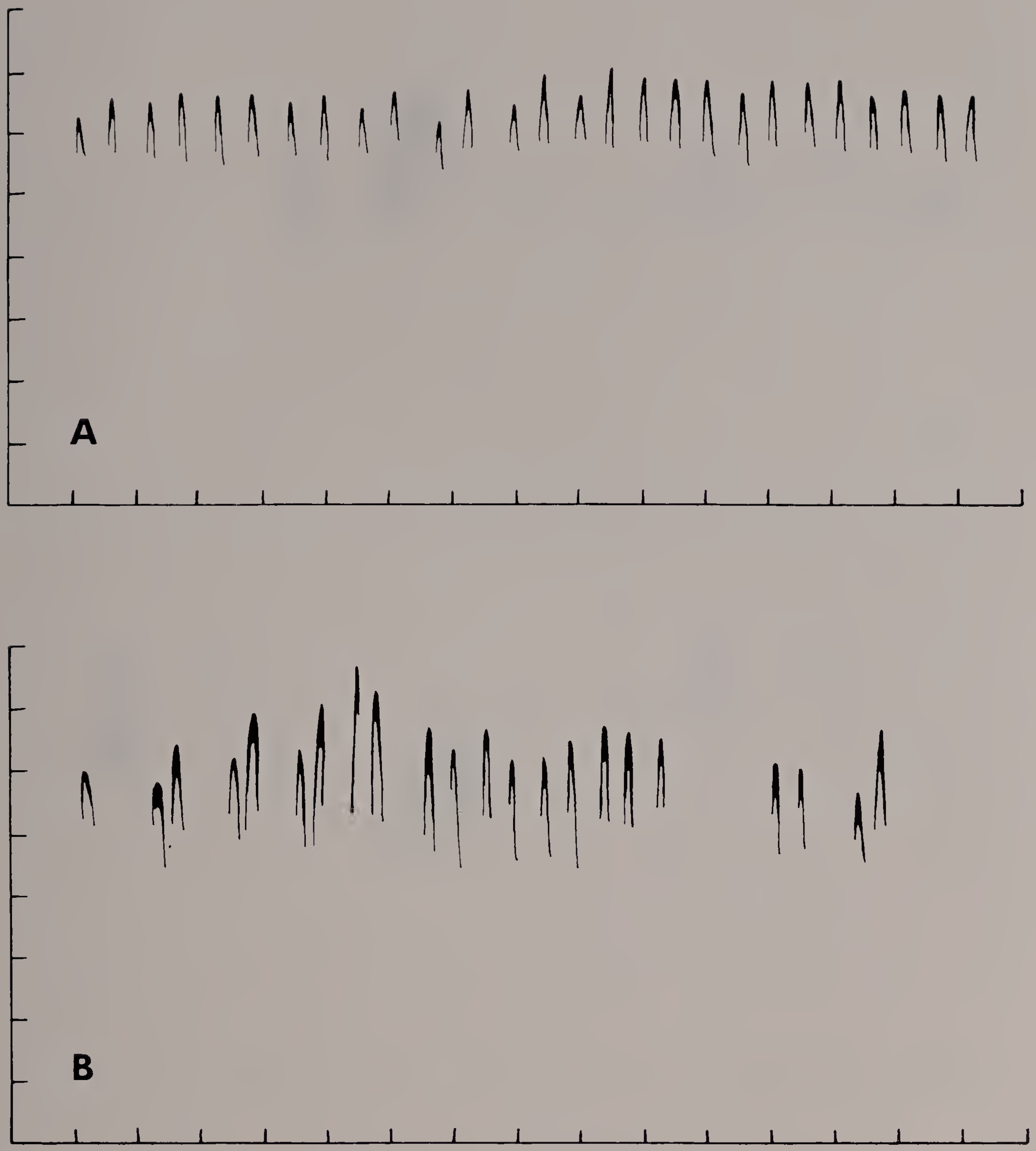
2:2c. ILHV by same male, perched after having made several attacks.

2:2d. ILHV/RV by same male, flying to attack the decoy.



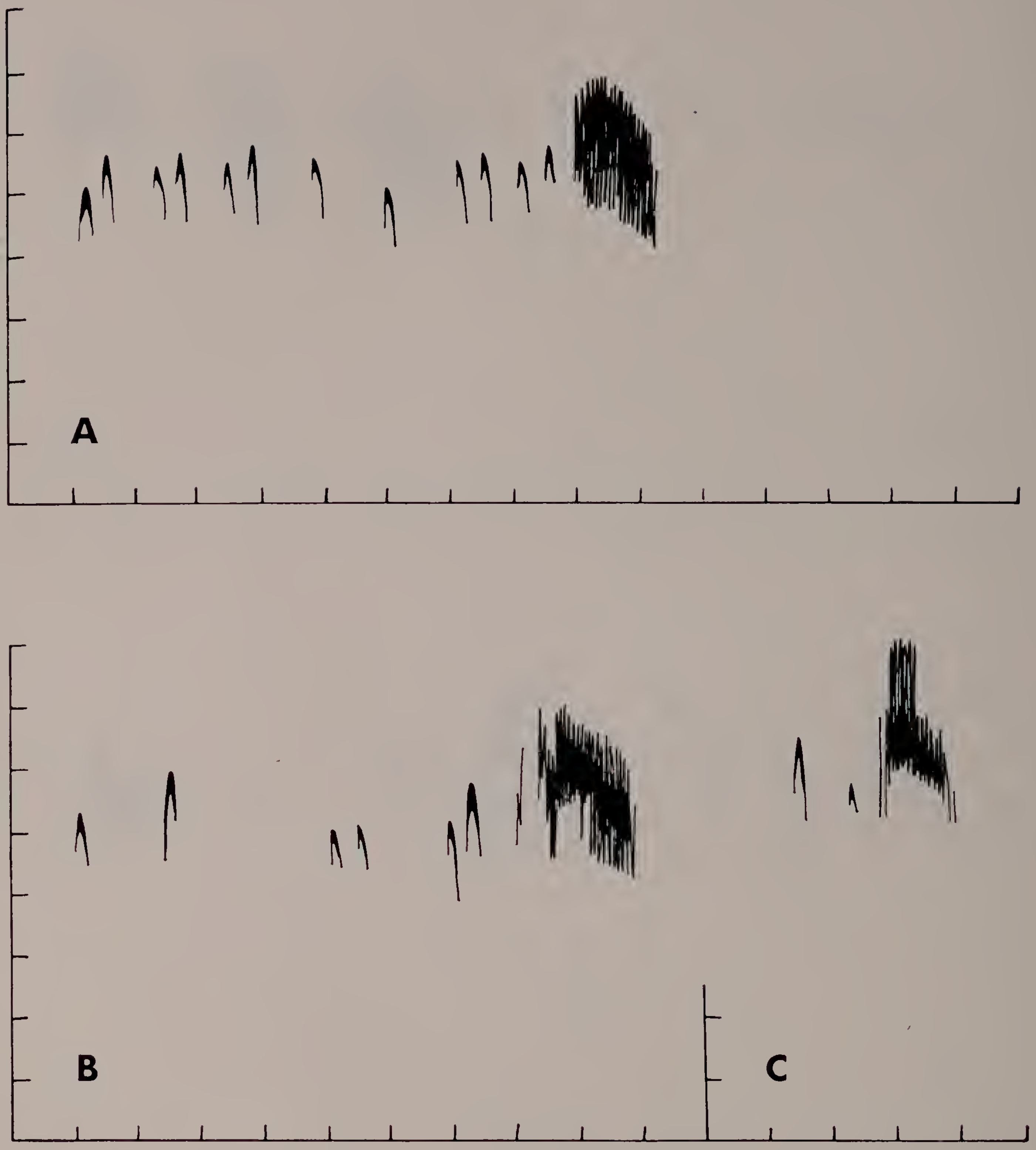
Tyrannus tyrannus

FIGURE 2:3a. Three examples (not consecutive) of RV.
2:3b. AeV, in a Tumble Flight.
2:3c. Single "tee" given by male just before fleeing as female oriole attacked him.
2:3d. Calls uttered by a male flying to attack a stuffed Little Owl (0.5 seconds of silence deleted between the first call and the subsequent burst); burst includes four Bill Snaps and calls of varying lengths, the shortest two sounding like "tzit."



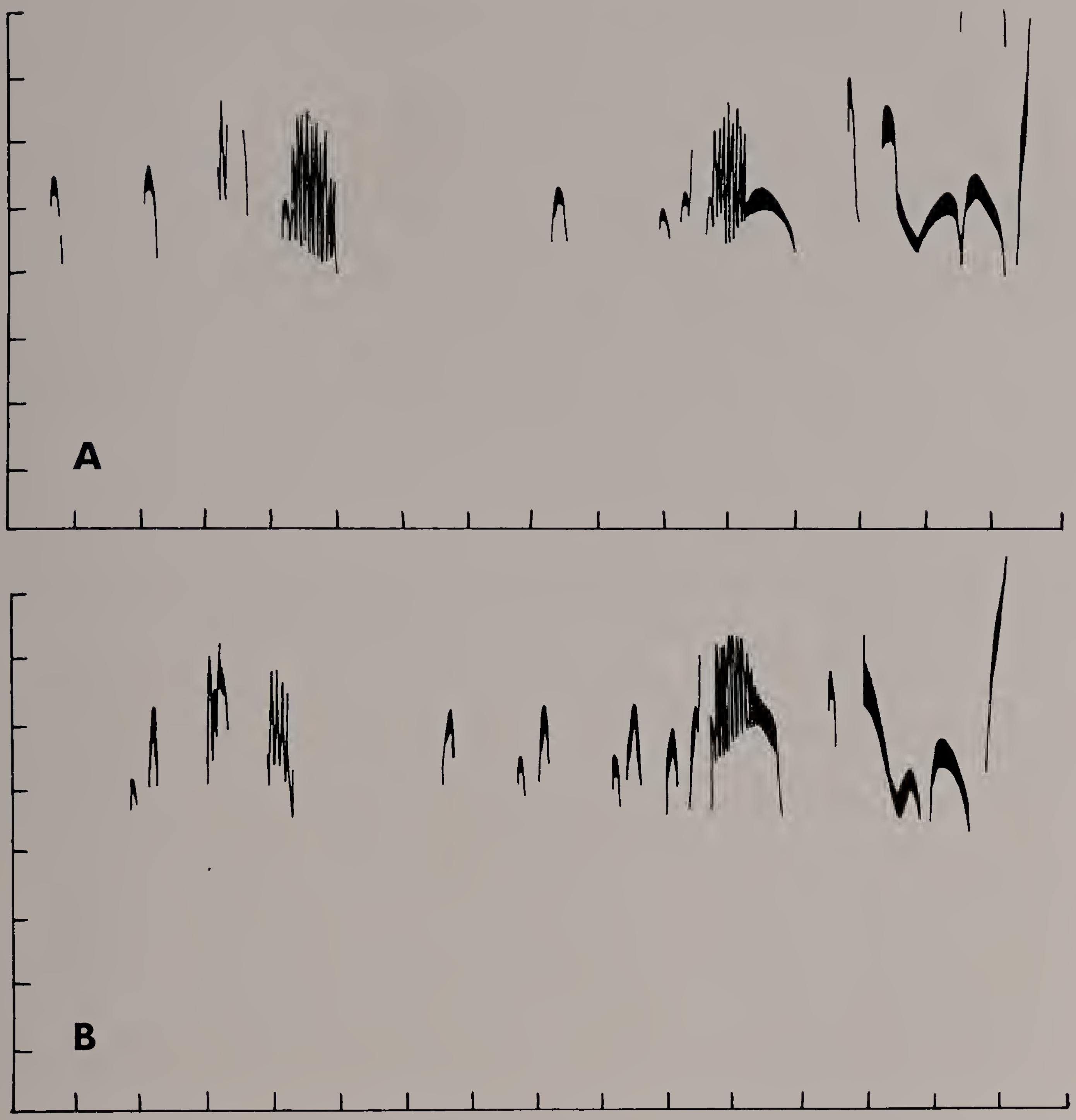
Tyrannus tyrannus

FIGURE 2:4a. Part of a prolonged CV, by a female.
2:4b. Couplet variation of CV, by a male.



Tyrannus tyrannus

FIGURE 2:5a. CdV, by an agitated, guarding male.
2:5b. CdV by same individual shortly after example (a); note how final units of CV merge with "zeer" portion.
2:5c. CdV, very brief example from same male. Note how the terminal "zeer" portions of all three examples are different.



Tyrannus tyrannus

FIGURE 2:6a. RRV (Massachusetts).
2:6b. RRV (Manitoba).

Chapter 3.

OTHER DISPLAYS; DISCUSSION

NON-VOCAL DISPLAYS

Tumble Flight

Description. In *T. tyrannus* the Tumble Flight is apparently given only by males. Typically, a bird takes flight, climbs at a slight angle and not necessarily rapidly, with a stiff, fluttering wing beat to about 40 to 60 feet above the vegetation, rapidly calling high-pitched ILHVs. After reaching full altitude, he rises sharply, stalls, twists, and falls from three to ten feet, flipping and twisting in a tight series of contortions that resembles an aerial face to face fight, although without an opponent. He then recovers and proceeds to or in the original direction for perhaps 30 feet, rising to another stall and tumble. Between tumbles he may not call at all, or may call an occasional ILHV. Just before the apex of the stall he gives an AeV; then he begins to fall, and with his head tucked down a bit, gives a series of three or four brief, clear, AeV calls (these may be replaced at times by high ILHVs). After his last tumble or stall the bird returns to his perch, often on fixed wings, sometimes with a series of long, shallow swoops. An unusual variant has been described by A. D. DuBois in Bent, 1942; the bird did not tumble forward but somersaulted backward as apparently sometimes happens in displays of *T. forficatus*, q.v.

Use. During the day the TF is most commonly seen after or during territorial encounters. A bird that has put a rival to flight will often perform a display with good tumbles, and then may attack the intruder again if he is still fairly near. On one occasion two males, which had fought several times between their nest trees, began to call ILHVs, and then went into TFs flying parallel about 40 feet apart. Again, in another dispute involving much Crouch display the defending male occasionally broke off and went up to about 40 feet in a silent flight which involved no real tumbles or twists but only slight stalls.

Indeed, the display is often given in forms which omit the tumbles, and sometimes even the twists, but it usually has a recognizable series of stalls or groups of stalls, and usually has high-pitched calling. Twice I have seen it performed by a bird returning from pursuit of a hawk —one a Sharp-shinned Hawk (*Accipiter striatus*), the other a Pigeon Hawk (*Falco columbarius*)—and in each case there were neither good tumbles nor twisting. Alternatively, a bird sometimes performs a low, rapid, erratic flight marked by sharp twists and turns and ILHVs. Occasionally in May, 1960, I saw flights in which the initial calls were RV, and the calls in the tumbles were CdV; this form seems to be extremely rare.

The TF is associated with both morning and evening twilight activity. In the morning it often both precedes the RRV and occurs in the active period that follows this vocalization. The TF is also associated with the darkness that precedes a heavy rainstorm at any time of day. In these times of relatively low light intensity tumbling and twisting are often (not always) omitted, even though the flight itself is likely to become rather erratic and fast. Actually there seems to be no correlation between a *fast* flight and the presence or absence of tumbling, but there is more and faster calling in a fast flight. In all cases, but especially in the twilight performances, taking flight is usually preceded by RVs which become higher in pitch and lead to ILHVs.

The TF is clearly an infectious display, particularly in the twilight periods when one individual rarely can give it without having two or three neighboring males rise and give it almost immediately, each apparently over his own territory. The male which displayed after returning from chasing the Sharp-shinned Hawk had scarcely started when two other males rose and gave the same version. At Delta I have even seen Western Kingbirds rise and give their closely similar homologue after a performance by an Eastern Kingbird, and the converse, too, occurs. One evening an Eastern Kingbird responded to a TF of a Western Kingbird by flying back and forth with much LHV before finally performing a TF (with six to eight foot tumbles), and then it chased a Western Kingbird.

The association of TF with territories should be noted. This is born out by the behavior of all the males in the two hawk chase incidents — they seemed to give the display as they entered their own territories, or at least as they approached their nest trees. After a fight the TF would be given by the bird who was on his own territory (if he won) and not by the intruder; in the case mentioned where two males both gave it after a fight, flying parallel, note that the intruder had first returned to his territory, that the fight had been a prolonged one, and that the birds were nearly evenly matched once on their own grounds.

This display apparently persists, again like the RRV, as long as the birds are on the breeding grounds, and it may be given in late August in the twilight periods. My fragmentary observations for the end of the season in Massachusetts suggest it is then much less frequent, but that the males may still be holding territory. It was true, both for this species and for *T. verticalis* in regions of high population density, that there is a resurgence of territorial intruding in the period just before fledging and while the fledglings are largely dependent, the intruders being adults apparently attracted by the insistent vocalizations of the young. This intruding leads to much defense and fighting and to very confused situations, and Tumble Flights become quite common for a few days.

It may be worthwhile to speculate on the tumbling part of the performance. The actions of the bird are so much like those he would go through if engaged in a fierce aerial face-to-face fight with another kingbird, and so little like any other movements I have ever seen a kingbird make, that it seems quite plausible that the display could represent the ritualization of fighting behavior. The bird at least appears to give a remarkable demonstration of "shadow-boxing."

Message and Meanings. The message of the Tumble Flight probably varies at least slightly in accordance with the completeness of the form and with the vocalization(s) accompanying it. The basic message, however, is likely similar to that of the RRV, as are the most probable meanings.

Displays Using Wing and Tail Movements

(1) Wing Flutter (WFt) and (2) Wing Flick (WFk). (1) When a perched bird gives the LHV vocalization, the wings are almost always extended laterally and fluttered rapidly. They are not quite fully opened; the elbows remain slightly bent, although the carpals are held out from the body, and the wing tips describe a quite small arc—such that the movement looks rather stiff. (2) In the Crouch display with WFk, on the other hand, the wing tips droop below the body and the carpals are held in close to the shoulders. In this case the primaries are sporadically flipped or flicked upward and both wings rotated forward in a single, quick movement, so that their dark upper surfaces are toward the opponent rather than the pale linings shown by the Wing Flutter.

That movement which is typically used within the pair is Wing Flutter, that typical of aggressive encounters is Wing Flick, yet there is no clear distinction between the two. In the presence of a mate various intermediates will occur if the situation contains strongly agonistic components, for instance, when an intruding male approaches a new pair, or when a potential predator approaches the brood. Such intermediates commonly involve passage of Wing Flicking into Wing Fluttering as attention is drawn from the primarily agonistic stimulus by some movement of the mate. As this change proceeds, the displaying bird will often straighten up from the Crouch position into the markedly upright stance of the WFt display, the speed of RV calling will increase, and the harshness becomes somewhat less; then an LHV may be given. Sometimes an agitated bird may respond to an LHV from its mate with the RV and a WFk or two, but without going into the Crouch. Displays in which the speed of fluttering is slow and irregular, and in which the carpals may be closer to the body than is usual for the WFt do occur, and it is sometimes difficult to say whether these are intermediates or incomplete forms of the WFt, although some are clearly the latter. In general, the fastest fluttering occurs when the wings are highest — that is, most nearly straight out to the sides. They are not held above the back in this species.

Use of the LHV in flight (fig. 3:la) is almost always accompanied by pulling the head back, and by a WFt in which the wings beat rapidly in a small arc lateral to the body and not above shoulder level. Such a stroke greatly slows the bird's forward speed, and since it has this additional, non-communicative function, it cannot be termed a "display" if we take the definition strictly. It resembles in an exaggerated way a stroke frequently used when a kingbird (of any of the species I've seen) is feeding in a swarm of insects, taking many in quick succession in a restricted area. Eastern Kingbirds, particularly males, tend to use a fairly shallow, fluttering stroke in much short distance flying, at least during the breeding season. It is convenient to refer to this as "hesitant flight," but it is not a display. At other times, such as in migration, a deeper stroke is used; this is used even in the breeding season for longer flights (particularly if the bird is not agitated) and for flights to attack or supplant.

While the WFt and WFk are connected by a spectrum of intermediates, it is useful to view them as two separate displays. Possibly both were derived from a single flight intention movement, or possibly they had independent evolutionary origins, and intermediates have arisen in the course of their association with other displays which may quickly succeed one another in time. If there were separate origins, I should presume that the WFk began as an intention movement of attack because it often precedes attack and occurs with the Crouch display, and because the motion could be followed by flying forward. The WFt could have come from a tendency to slow flight down to a hover when approaching another bird (since this is essentially what it accomplishes in flight) under the conditions of a relative increase in approach hesitancy. It is clearly less associated with the likelihood of attack and more with the LHV. The upright pose and motions of a bird Wing Fluttering while perched would facilitate a quick about turn and flight away. Perhaps it is simpler, however, to presume a single flight intention movement as the origin of both, with divergence due to increased signal value in two different situations, and to the different directions of flight each favors.

The message and meanings of the WFt are probably the same as those of some LHVs, not including the modifications introduced to the LHV message by harshness or AeV forms. The message of the WFk is likely that the communicator is becoming ready to attack (but not as ready as when the Crouch display is also being given).

(3) Wing Whirr. Occasionally in a chase of undetermined nature I have heard one of the birds make a loud, rather brief, whirring sound with its wings. Once a female which landed unusually near me suddenly flew off as if startled and gave a loud Wing Whirr (I was in a

much used observing position near her nest). In another instance, two males, which were displaying vigorously toward one another with the Crouch (including WFk), were making frequent short flights of one to three feet among the branches. In such flights they occasionally gave loud Wing Whirrs; males have especially attenuated outer primaries which might facilitate the production of this sound. When one made such a noise the other was likely to do it almost immediately afterward. The males seemed well matched.

From so few observations it is difficult to detect a pattern in this apparently rare display. Possibly the Wing Whirr had its origin in the WFt, making it more conspicuous. It may indicate a hesitant flight in which the bird has intense and conflicting motivations, but it is too early to guess at its message and meanings.

(4) Tail Quiver and (5) Tail Flick. Both WFt and WFk are accompanied by synchronized tail movements. During WFt the tail is spread slightly and quivered up and down, describing a very small arc. With WFk it is more widely spread as it is flicked forward over the back in an exaggerated fashion, spreading fully as it goes, and thus displaying the banded tip and very narrow white outer margins.

These displays might be named Tail Quiver and Tail Flick, since both sometimes occur independently of any wing movement, as when a bird peers at a possible predator and calls an occasional RV with a quick single Tail Flick. Such situations are agonistic and, with greater provocation, may lead to Crouch displays. Occasionally during the transition the bird may partially spread its tail and at the same time give a slight WFk. Finally, the low pitched form of the CV usually has with each element a quick, slight, flick of the tail which is between a flick and a quiver, but there is no wing movement.

The messages of these tail movements are likely the same as the coincident wing movements, and less intense when the wing movements are absent.

Crouch Posture

Description. In the Crouch Posture the bird adopts an exaggerated pose in which the legs are bent and the body is held horizontal (fig. 3:1b). The neck may be extended, with the head pointed toward the adversary and the bill at a downward angle. The Crown Ruffled occurs, but usually with no Revealed Crown Patch. The back is ruffled progressively forward from the rump as the underlying musculature contracts. The flanks are ruffled, the chest is not, and the throat is usually ruffled. The wings are drooped and flicked, and the tail is spread, making the terminal white band conspicuous (when fully spread it also shows narrow white outer margins). The tail is usually held level or a bit above the level (see fig. 3:1b), and also is flicked. Orientation movements of the bird, or of just its head, toward its opponent are common, as is a shifting of the bird from side to side — in contrast to orientation and lack of shifting during an LHV exchange.

Use. The most common occurrence seems to be in territorial disputes. Indeed, it is almost never seen after the period of pair formation through nest building. Early in the season at Delta while territories were being defined and the first territories were being reduced in size as more males arrived, fights between pairs were common (a period of less than three weeks for the population as a whole). Often these would involve all four birds, although only two (presumed males) would be pitted against each other while the others sat on opposite sides of the encounter as spectators. If the two antagonists displayed vigorously, aerial fights would be frequent, the opponents meeting face to face and tumbling down as they struggled, and then breaking apart. After a brief chase both would land, display, and rise again in an aerial fight.

In such a case both birds would meet part way between the two nest trees, perch a foot or two apart, and adopt the Crouch pose and movements. They would change their orientations frequently, sometimes facing, sometimes not quite, shifting about on their perches, or changing to perches within one to three feet of each other. Both birds at such times repeat the harsh RV, and also use the CdV frequently. The watching mates call less frequently, primarily the ILHV, and clearly distract the two central birds, who may also give higher calls or will often turn to face them, switching from the Crouch posture. If the mates are using LHV and WFt, this will be answered before the males turn to one another again. Occasionally one of the females will join in, usually when the males are actually fighting, and dart about the edge of the fight briefly, apparently without ever becoming thoroughly involved.

When the displaying birds are within a foot of each other, the situation seems particularly acute, and there is much maneuvering on the perches so that the birds are often not directly facing each other. Once they face each other, a close, tumbling fight usually follows. Occasionally one Gapes just when facing, his bill pointed slightly downward. The victor of a fight may give a Tumble Flight display.

Toward midday, or by the time nest building was underway, less violent encounters were more the rule at Delta. Usually these would involve only one pair and a male, or just two males. One of the males was sometimes more aggressive than the other, but this might be either the intruder or the defender. One bird might not display at all, nor even face the other, who would then stop displaying. Calling was less frequent and consisted almost entirely of the harsh RV, the CdV being very rare. Movements and maneuvering were also less frequent and less pronounced, and facing with the whole body was rare, although occasionally necks were turned so that the birds faced with their heads. When four birds were present, activity might still lag, but periodic, very short fights were more likely. In one such instance one of the males occasionally flew off in a weak Tumble Flight (without tumbles, only slight stalls and no calling) and would return and continue the Crouch display with his opponent. The last time I noted use of the full display was on 21 June when a bird whose mate was lining a nest flew past 30 feet from another pair on his way to the nest site. He called a high, emphatic series of RV and an LHV as did one of the pair. This latter individual (but not its mate) went into a full Crouch posture.

Within the pair the Crouch seems to be rare. Early in the season, while claimed territories were in a state of considerable flux, a (presumed) male met his mate at a point where he had been repeatedly fighting with a rival, and began to go into the posture. His mate, however, did not display but turned her head slightly away, and he straightened up. Again, even earlier in the pair formation period, I watched for several hours a (presumed) male repeatedly approach his mate. The two birds used primarily the LHV and its postural accompaniments, although the female might occasionally substitute a few ILHVs for the LHV. The male frequently chased her and gave the LHV, while she fled (not rapidly as a routed rival would have), calling less. Then they would land and, not directly facing, give the LHV with its posture and movements. Gradually the male's chases became more aggressive, perhaps partly or largely due to the fact that he was constantly interrupting his approaches to the female to fight and chase off an intruding Eastern Kingbird. As he became more aggressive toward the female she began not to fold her tail after LHV displaying, to let her wings droop, and occasionally even to flick them. That is, she began to produce intermediates between Crouch and LHV posturing. The Crouch shares with the LHV the ruffling of the crown and adds other ruffling and fluffing, replaces WFt with WFk, and adds the crouching. She kept her head fully erect and did not actually crouch down except once when the male tried to mount her. She then faced him, Gaping over her shoulder, calling a very harsh CV and crouching partly, but giving the WFt instead of the WFk of the Crouch display. Other copulation attempts were seen in various pairs when females did a partial Crouch; it seems likely that such a posture can be confused by a male with the female precopulatory position.

Finally, in some cases the display seemed to be used toward me. One case involved a (presumed) male in highly agitated nest-site-showing display with harsh RV, LHV in flight, and rare CdV. Often his Crown was Ruffled and his tail spread, and he leaned forward approaching the Crouch posture, but without orientation toward me or any recognizable stimulus. At least once, though, he did adopt a full Crouch, with WFk and Tail Flicks, directed toward me. I was standing about 30 feet away. In another instance I approached a nest, which a female was lining, and her mate flew to the top of the tree where he called the ILHV frequently. She came off the nest, perched ten feet below him, wiped her bill a great deal, and then went forward into a Crouch but with only the throat ruffled. After a few seconds she straightened up, and a minute later flew away. On 22 July, 1960, a pair became very agitated when I approached their young (nine days out of the nest); they approached me with harsh RVs and would occasionally face me with a Crown Ruffled and would then give a few quick WFk, while leaning forward.

Message and Evolutionary Origin. The Crouch is always given in agonistic situations in which fights are quite possible. Its message seems to be "I have a strong aggressive tendency, and may attack the individual toward which I am facing." The evolutionary origins of the crouching and of the orientation of the head and body toward the opponent have quite possibly been intention movements of attack. The slight downward angle of the bill may be related, as in gulls (Tinbergen, 1959) and many other birds, to a pecking intention movement of some sort.

Revealed Crown Patch (RCP) and Raised RCP

The Eastern Kingbird has in the center of its crown a patch of brilliant orange or orange-red feathers normally concealed by the more lateral crown feathers. This patch can be exposed by parting the overlying feathers (RCP), and can be made more conspicuous by erecting the bright feathers as a sharp crest (RRCP). I am quite sure, although surprised, that both these displays are used infrequently. I have seen them only in the vicinity of the nest from the time of incubation on.

On a few occasions RRCP was used as a display between the members of a pair, and in all cases I think the female initiated it. It might occur if she returned from foraging and found her guarding mate perching on the rim of the nest. This was not an unusual situation in at least one pair, and was most often dealt with without use of the crown patch, by a simple thrust at his chest, or with some form of the CV. RCP or RRCP might also be used if the pair was agitated and the male turned on his mate in some fashion, but again, this was usually dealt with by an LHV. When the display(s) were used in the pair they immediately elicited a like response from the mate, and were then usually terminated promptly.

On other occasions I have seen a male drive birds such as Red-winged Blackbirds (*Agelaius phoeniceus*) from the nest tree, flash the patch in attack, and perhaps keep it erect for some minutes afterwards. However, usually it is not flashed in such situations. Females do not usually display at all when driving such birds away, but I did see one who was particularly disturbed by a pair of House Wrens nesting a foot above her nest, and who seemed to be an overly aggressive individual, occasionally use RCP toward a wren.

Davis (1941) saw these displays only in intra-species situations, not in attacks on other species. In Bent (1942) are accounts in which they were used by a victorious male after defeating a rival, and in which they were used toward an observer approaching a nest.

In appearance the displays suggest a gaping mouth to me, and to other observers who have commented upon this. In fact, the feathers are about the color of the gape of the species, and they may be mimicking it. Carrying a message of aggression, the displays may increase the threatening value of Gaping by doubling the number of open "mouths" seen by the recipient. (Doubling of a frightening stimulus is not unknown. N. Tinbergen has told me (*pers. comm.*) of caterpillars that have two pairs of spots that mimic snake eyes.) If the displays indeed operate by mimicking the Gape display, then it is less surprising that they are so rarely used, for most mimicry seems best employed with parsimony. Where central crown feathers in other species of tyrannids are not the color of the gape (as, for instance, in various species of the genera *Elaenia* and *Serpophaga*), then they may always be exposed, and may even be erected fairly commonly. It is because of such species, incidentally, that I suggest the adoption of the two terms RCP and RRCP, since the displays are in these cases clearly distinct from one another. Even in *T. tyrannus,* the RRCP does not inevitably follow the RCP.

Crown Ruffled and Other Plumage Signals

Quite in contrast to the RCP is the Crown Ruffled, a display in which the dark outer feathers of the crown are fluffed or ruffled. This is extremely common. It is invariably used with both the LHV and the Crouch, almost invariably with the ILHV and RV, and with all but the very high form of the CV. It is even common in the absence of any other displays when a bird merely becomes aware of some change in the environment which is not yet of any apparent significance. While it can vary from a simple fluffing to a very marked ruffling in which the feathers are alternately erected and lowered, the change appears to be continuous. Even the most extreme forms continue to conceal the brilliant feathers underneath. With so general a usage, its message can only be one of unspecified anxiety of varying degrees.

At least at times the Crown Ruffled can be accompanied by a fluffing or ruffling of the throat. In my observations this seems to occur sporadically in agonistic situations, but I was rarely sure I was not missing it — it may often be rather hard to detect in the field. Pending further information this display remains unnamed.

A slight general fluffing of all body feathers may also have often gone unnoticed. It does occur in agonistic situations. The opposite, a pronounced sleeking of body feathers, occurs in some agonistic situations when the bird is not otherwise displaying; such a bird is just about to fly, and usually flees or at least does not attack. Whether or not this is a ritualized feather posture cannot be ascertained as yet. Certain other plumage alterations of the back and flanks are apparently peculiar to the Crouch posture, and are described thereunder.

Gape and Bill Snap

Two displays by the aggressor often immediately precede attack in the order Gape, Bill Snap, attack. At times Gaping may be quite effective in preventing attack; on several occasions I have seen a female repulse what appeared to be attempted mounting by her mate by Crouching, turning her head, and Gaping over her shoulder at him. Bill Snap, however, is limited to birds that are in the act of attacking. The display is a loud, abrupt sound made by bringing the mandibles sharply together with the maxillae. Often it is preceded by no other displays, as when a female launches a vehement attack from the nest on some approaching blackbird in the absence of her guarding mate.

Both Gape and Bill Snap displays are widely distributed among birds in general, and are usually postulated to have been ritualized from intention movements of biting. The message of Gape probably includes some measure of hesitancy about attack, but a Bill Snapping bird is committed to at least an attack approach. Observations of birds attacking stuffed owls and, at times, attacking me, indicate that if the object of attack does not flee the attack may abort short of contact, even though the Bill Snap is used during the approach.

Displays of Nestlings and Fledglings

Since it was rarely my practice to disturb kingbirds by closely inspecting their nests, and since I spent little time in the field once there were fledglings about (other than in 1960), I have only fragmentary information on this subject. Very young nestlings seem to be silent, but soon develop a begging call which is thin, rather variable, and slightly rasping; they retain this long after they leave the nest (fig. 3:2a). By at least the eleventh day of age another faint vocalization becomes recognizable. It is a little louder and shorter than the begging lisp and has two discernible elements. This is an ILHV, although it is not identical with adult forms (fig. 3:2b). The begging lisp is a "zee" element of the same type of vocalization, usually quite prolonged, and descending farther than it does in adult forms of the ILHV. It often tends to break into two humps, very much in the fashion of some of the intermediates that adults may produce when passing from a string of ILHVs into an LHV. At first, the ILHV is used by hungry nestlings each time a parent appears on a perch above the nest; they switch to the begging lisp as the parent drops down to the nest to feed them, and may use the ILHV again as the parent departs. It is also used in the prolonged absence of the parents, or if an observer handles a nestling. Eventually it largely replaces the begging call, and even after the young have been fledged for many days, this vocalization does not seem to elicit agonistic responses from the parents.

Nestlings about to fledge become very vocal, persistently repeating mostly their species specific (but recognizably juvenile) ILHV. This noisiness persists for at least several days after fledging, and apparently excites and attracts neighboring adults as well as their own parents. At about the time of fledging, young also begin to use a harsh vocalization (fig. 3:2c) which is like a brief RV. Sometimes it is used when a young kingbird has lost its balance and is fluttering hard to regain it, and sometimes it is used in an awkward landing — both instances suggesting that it may be an aggressive reaction to frustration, as some adult uses of the RV appear to be. Occasionally it was used very faintly when I could correlate it with no activity or state; many more observations will be needed before this vocalization can be understood.

Once parents begin to react to persistent chasing by fully fledged young by occasionally turning on them aggressively, the LHV develops. Perhaps this LHV is formed through some sort of hybrid between the ILHV and the two-humped form of the begging call, but I do not have recorded material with which to check this. So far as is known, no other vocalizations develop in the young at this stage, and these may be all they have before entering the silent months of fall and winter. I have not noted whether or not such plumage erection displays as Crown Ruffled are developed by the fledglings, and the only visible display I have seen is the WFt which accompanies LHV. They do not, as do many of the oscines, flutter their wings when food begging.

The initial begging lisp must carry the message that the nestling is hungry. It is unlikely that this lisp is unambiguously species-specific (which is unimportant, as its principal use is by nestlings), but the ILHV that begins to develop a few days before fledging is certainly species-specific. Its message is thus more detailed — the caller is an uncomfortable, juvenile Eastern Kingbird. It is probably hungry, but since the call can be elicited by an observer picking up the young bird, we cannot be sure that the message refers specifically to hunger and not to a more general state of discomfort.

Discussion of Communication Pattern

The social problems faced by a Kingbird at the beginning of a breeding season have already been mentioned in Chapter 1. It should be apparent that the set of messages inferred for the 19 displays described are, taken by themselves, inadequate to enable an individual kingbird to get through a breeding cycle. But a message encodes only some feature(s) of the mood of the calling bird. Taken in the broader context of events within which it occurs, and against a background of genetic and experiential information, the message adds a feature to this context which must often be extremely important — it permits a more accurate prediction of the subsequent activity of the communicating individual. To the recipient, the context of the message is both unavoidable and critically important, and it enables most messages to have, for any one recipient, a variety of meanings in different contexts. This relationship of message, meaning, and context has been described more fully in earlier papers (Smith, 1963, 1965). The question with which we must be concerned here is what sorts of meanings are available to Eastern Kingbirds using the repertoire and pattern of communication that have been outlined, and are these meanings sufficient for the social needs of the species?

To facilitate the understanding of how meanings are generated, most of the more important situations have already been mentioned in the foregoing as each display has been described. Others are fairly easy to infer, knowing the circumstances surrounding the use of any particular display at any particular time. Let us look now at the social problems accruing to the breeding season, and at the usages of the kingbirds' repertoire, to see if the signals are employed in a fashion that will permit the generation of a set of meanings appropriate to the task. The chronological arrangement of the problems presented in Chapter 1 is useful in helping us to visualize the situation as it occurs in nature, but it should be evident that similar problems recur at various stages. To simplify our analysis, we can present a set of social problems as an interrelated pattern having seven main divisions: advertisement (subsuming attraction and repulsion of conspecifics), individual recognition, appeasement and reassurance, threat, giving of information to conspecifics with which to monitor the environment, alerting of the partner in the pair, and association with the offspring during their dependent development.

The seven problems of this set point to seven basic functions that accrue in part to the displays system employed by the species. These will be discussed later in this chapter, but they do not correspond closely to the set of messages we have inferred. However, at least the size of the message set exceeds the size of the problem set when viewed in this fashion. The set of messages can be roughly paraphrased (even with more knowledge, an exact translation would be elusive) as follows:

LHV: I, an Eastern Kingbird, am experiencing some conflict with a tendency to locomote.

ILHV: I, an Eastern Kingbird, am experiencing some interference with a tendency to locomote; total tendency less than in the LHV.

RV: I am experiencing at least partly similar tendencies to the ILHV state, and am more likely to be defensive. I am an Eastern Kingbird. (Harsh forms:) progressively less ILHV message, and a change from defensive to offensive aggressiveness, probably with a loss of species-specificity.

AeV: I, an Eastern Kingbird, am a frustrated fighter.

CV: I am anxious over an ambiguous but potentially disruptive situation in which the nest site, nest, mate, or offspring are important.

CdV: I, an Eastern Kingbird, am anxious and at least defensively aggressive over some situation concerning the nest or territory.

RRV: I, a male Eastern Kingbird, am in breeding condition and defensively inclined over a territory. (Clues about individual identification are also almost certainly included.)

WFt: (probably the same as for LHV.)

WFk: I am aggressive, but at least somewhat inhibited.

Wing Whirr: I am flying (more detailed inference not yet possible with the few data available).

Tail Quiver: (probably low intensity LHV message when used without other displays, LHV message when used with other displays.)

Tail Flick: (probably low intensity WFk message when used alone, WFk message when used with other displays.)

Crouch: I have a strong aggressive tendency, and may attack the individual toward which I am facing.

RCP: I am very likely to attack. (RRCP: I am even more likely to attack.)

Crown Ruffled: I am anxious.

Gape: I am about to attack (probability slightly less than in RCP).

Bill Snap: I am attacking, but may still be just slightly hesitant.

Tumble Flight: (Basic message probably similar to that of RRV, perhaps with a stronger aggressive component. The flight is never silent, and its message must be modifiable to a considerable degree by the different vocalizations which accompany it; for one thing, similar flights occur in some other species of the genus, but some of the vocalizations are species-specific. Additional modification of the message must come through varying the extent of at least the "tumble" portion.)

Begging lisp of offspring: I am hungry. (If it occurs mostly when a parent returns to the nest, it may include the additional message: I probably perceive a parent.)

ILHV of offspring: I, a juvenile Eastern Kingbird, am uncomfortable (probably hungry).

When the messages of this set are placed in all of their possible contexts, a much larger set of meanings results. These meanings should be stated, following Cherry's (1957) definition, in terms of observable responses, and an enormous amount of observation would be required to demonstrate that all of the possible responses do occur. Further, the responses would have to be arranged according to sets of probabilities for each major context in which a display occurs, as it would be an impossible task to learn *all* of the relevant immediate and historical context for each observation. Even to state all of the possible observable meanings would take an inordinate amount of space, and is, in fact, unnecessary. It is much simpler to note that a bird behaves *as if* it had obtained and assessed certain information derived from a display in a context, and to describe this inferred assessment (which, to the extent it does exist, is also a "meaning"). This is not to conclude that a bird "assesses" situations in the conscious and logical manner we at times employ, and there is certainly no reason to believe that syntactically phrased statements such as I employ below closely represent avian mental states. Nonetheless, birds do behave *as if* they were acting upon assessments which can be stated this way by us. Birds do perform operations on sensory inputs, and the results are as if the operations had been assessments.

The following should be viewed as a list of purely hypothetical mental states intermediate between the processing of sensory inputs and the generation of observable responses (meanings which can be identified). For the first entry in the list some observable meanings will be derived to illustrate just how progressively more knowledge of the total sets of possible context for each entry can lead to the prediction of a range of probabilities of different responses.

LHV: (1) I am not likely to be attacked by the approaching, vocalizing conspecific individual.

(Depending upon the identity of the recipient, this hypothetical "assessment," phrased as only a human would phrase it, might lead to various observable responses which we could interpret as meanings. For instance, an adult conspecific of the opposite sex, in breeding state and established as the communicator's mate, would probably repeat the signal (or at least some form of the LHV and attendant displays) and not flee, although there are measurable but much lower probabilities of other responses in some variations of this context. These rather improbable reactions would be meanings in the same sense as the most probable reaction, but are usually less important at our level of analysis. Suppose, however, that while the recipient is an adult the approaching conspecific communicator is not its mate but one of its offspring, perhaps a fledgling of ten days. Now the response may be avoidance, it may be to ignore the approaching bird, or it may even be aggressive; the probabilities of each of these different meanings can only be known after an extremely thorough set of observations of the different contexts.)

(2) (Harsh form:) I am being approached by a bird which may not attack me, but which is aggressive.

(3) I am being followed for some reason other than attack. (In various different contexts the follower can be a mate, an offspring, etc.)

(4) The calling bird is a patrolling male, hence (a) I may approach and try to form a pair bond (recipient an unpaired female), (b) I must not intrude unless ready to fight (recipient a territorially inclined male), or (c) I must not display (recipient a non-aggressive individual which is a migrant, a foraging neighbor, or a member of the local floating population).

(5) My mate has left the nest unguarded (recipient a male who is not guarding), and I should guard.

(6) My mate or neighbor has become unusually active, and is disturbed by (a) the calls or activity of a neighbor, (b) the intrusion into the territory of a conspecific, (c) the presence of a potential predator, or (d) other. (Context will not always be sufficient for the recipient to perceive the reason for the mate's unusual activity.)

ILHV: (Presumably low intensity versions of (1), (4), and (6) of the LHV. By low intensity I mean that the communicator is signifying less intense tendencies to do any socially relevant activities.)

In addition, the ILHV in certain contexts may indicate that an animal which is holding the communicator's attention is potentially dangerous.

RV: (1) The communicator is attacking or likely to attack (a) the recipient, or (b) one of the set of recipients.

(2) The communicator is a patrolling male Eastern Kingbird (see LHV, (4)).

(3) The communicator is in a guarding mood (discussed below). At low rates of RV repetition the recipient can "assume" that nothing untoward has been noticed in the territory; at higher rates no related assumption is possible, since the communicator may either have perceived an intruder of some sort or may be more aggressive due to an endogenously cycling mood (recurrent moods of this sort discussed by Wells, 1957, among others).

AeV: (1) In a fight, the communicator is losing and about to flee.

(2) In a Tumble Flight, the communicator is a male advertising as in LHV (4) but is probably rather aggressive and will be at least briefly "unstable."

CV: (1) There is some possible problem concerning (a) the nest or nest site, or (b) the offspring. (The indication may often be more specific than this, in that the stimulus viewed as a potential problem may be knowable. Probabilities of particular reactions of the communicator are not included, however.)

(2) The communicator is ready to form a pair bond, or possibly to copulate (in the case of a male who is nest site showing).

CdV: (1) (As in CV (1), but some probability that the communicator may become aggressive.)

(2) The communicator is a patrolling male Eastern Kingbird (see LHV (4)).

(3) The communicator, an opponent in a fight, is not fully committed to fight, but may become so at any instant.

RRV: The communicator is a male Eastern Kingbird on his territory and is (a) likely ready to copulate with his mate; he is probably individually recognizable and will be known by a female recipient to be her mate or a neighbor, or (b) (probable indication to a male recipient) ready to oppose transgressors. If the call does render individual recognition possible, then all males will know each morning if the position or identity of any of their neighbors has changed.

WFt: (Probably the same as for LHV.)

WFk: The communicator is aggressive, but not likely to attack. (Degree of probability of attack is expressed by other simultaneous displays, if any.)

Wing Whirr: (Although the reason that the communicator is flying may be important to the recipient, no detailed meanings can be inferred as yet from my data.)

Tail Quiver: (1) When used alone indicates only that there is some slight possibility that the communicator will fly, and various contexts likely suggest reasons for this.

(2) As for LHV when used with that vocalization.

Tail Flick: The communicator may attack, but the probability is low; see WFk.

Crouch: The communicator is strongly aggressive toward the individual it is facing or nearly facing, but is somewhat inhibited from attacking. (If there is more than one recipient, the meaning for each will be different; one will be the opponent and the others will be spectators.)

RCP: As in Crouch, but probability of attack higher; higher yet with RRCP.

Crown Ruffled: Communicator is aware of some potentially disruptive influence. (Some contexts will yield more precise meanings.)

Gape: (As in RCP, but probability of attack slightly less.)

Bill Snap: The recipient is being attacked by an only slightly inhibited communicating individual. (In the case of more than one recipient, others will be spectators and take different meanings from the event.) Since the communicator is attacking at the time, the display signals are largely redundant information, adding only its slight measure of hesitance.

Tumble Flight: (Meanings of the maneuver probably similar to RRV, although probability of subsequent aggression by the communicator is higher. Meanings vary as display, and hence as message, is varied; see message discussion above.)

Begging lisp: Feed the calling young Eastern Kingbird. (Species is known because (a) the communicator is in the nest, or (b) has the correct plumage.)

ILHV of offspring: Feed the young Eastern Kingbird which calls (it may be necessary to locate it first).

As has been said, some meanings at least can be verified by observing the behavior of display recipients. In most cases the recipient will either act on the basis of several displays that have been received since his last action, or will make no overt response, and one can only assume that there may have been an internal response, a modification of mood of some sort. Because of the complexity of the recipient animal and the number of possible responses open to it, a direct interpretation of meaning is rarely possible. In order to continue to exist, however, a bird must always be processing information from its environment and acting in ways appropriate to survival and reproduction, and its successful choice of appropriate actions indicates that "assessments" and meanings such as those suggested must be being used, although it does not tell us which meanings accrue to which displays.

Advertising

Consider now the set of seven main social problems, of which the first is advertising, which subsumes the problems of attracting and repelling conspecifics. If this problem were viewed broadly it could subsume all of the other communications problems, but I intend only that it deal with the social necessity of bringing together two conspecifics to form a pair, while excluding individuals which might interfere with either the formation or stability of the pair bond, or with subsequent requirements of the family.

The messages of at least the LHV, ILHV, RV, CdV, RRV and AeV (at least when used in the Tumble Flight) are relevant to this problem. Used separately or together at appropriate times, as already described, these displays will convey in all the necessary situations the identity and moods of the males who must advertise. From the list of possible "assessments" it would seem that the most relevant are those displays used in patrolling (primarily the CdV, LHV and ILHV), guarding (primarily RV), and two displays which are really specialized as advertisements, the RRV and Tumble Flight. The last is the only nonvocal display (it has vocal accompaniment) which is prominent in advertising, and it is particularly adept for broadcast dissemination of the advertising messages. The RRV, on the other hand, may be adapted for use at a time of such low light intensity that the displaying individual could not profitably engage in any other activity. This display usually has the most rigidly fixed form of all the displays of the species, perhaps partly because its messages are so critical, and partly because it is given at a time when there is no visible context available to supplement it. Stereotypy under conditions of low light intensity may be necessary, and has been proposed by Moynihan (1964) to account for the characteristic form of vocalizations in the Night Monkey (*Aotus trivirgatus.*)

The function of restless patrolling on the part of territorial males is to increase the probability of their coming into contact with conspecifics which may try to encroach upon the territory (other males) or enter it and form a pair bond (females). Although only one of the latter need be met with if a pair bond results, the necessity of repulsing other males remains if the pair bond is to be maintained — I have mentioned the persistent attempts intruding males may make to mount an already paired female. The function of displaying during such patrolling must be (a) to increase or decrease the probabilities of contact, and (b) to make more predictable to other conspecifics the mood of the communicator. In changing the probabilities of contact the displays may at first attract both females and males, but once the identity and roughly defined territorial claims of neighbors are known, males apparently begin to avoid contact. Once a male is paired and has established his territorial rights, patrolling becomes both less necessary and less frequent, although rights are to some degree reaffirmed daily. Since the establishment of pair bonds and of territorial rights takes place simultaneously and coincidently with the period of maximum daytime patrolling, a female can take the indication "possibly unmated" from displays used in such patrolling.

If a patrolling male is initially attractive to males as well as females (a supposition based on the facts that (a) males are drawn into encounters with one another, and (b) patrolling activity, as well as RRV and Tumble Flight usage, by one male often is followed by similar behavior on the part of nearby individuals), then the possibility follows that advertising males will tend to form clusters. That is, in an area of suitable habitat having an insufficient population of males to fill it, the males might tend to clump their territories together, within hearing range of one another. Lacking a full understanding of habitat preferences, this is difficult to measure, but it seems to have been found in other flycatchers by Kendeigh (1947, for the species *Empidonax minimus*). Some advantages would accrue to such clumping if the males could alert one another to danger, and if they stimulated each other into more persistent displaying (as at Delta, as contrasted with New Hampshire), thereby making it easier for migrating females to locate them. A system such as this would provide a convenient origin for the evolution of lek behavior.

The problems of advertising, in the sense used here, are those usually met with in oscines by the vocalization called "song." Marler (1960) among others, has discussed the functions of song: mate selection and possibly pair bond maintenance, individual recognition, and the repulsion of intruders are among the most important. These require meanings such as can be derived from my proposed "assessments" for the RRV and some cases of the Tumble Flight, and these two displays (especially the former) are the closest to "song" that a kingbird has. Yet song, when either functionally defined or defined on the basis of complexity of form (the two usages have led to considerable ambiguity in the ornithological literature) is not restricted to the predawn twilight as is the RRV. Throughout the day *T. tyrannus* does not "sing" in either sense, but continues to advertise. The CdV, which in form is often identical to the first RRV phrase, assumes much of the advertising function, but may be weak in characteristics useful for individual recognition, does not *invariably* signify "male," and has other, non-advertising functions. Similarly, the RV, the final unit in a CdV or RRV phrase one, also takes up *some* of the functions of song during the day, and adds other functions to these. Both CdV and RV sometimes occur in or before Tumble Flights, but the latter display usually makes use of the AeV, which resembles in form and sound the ultimate elements of phrase two of the RRV, but which also occurs in another, non-advertising usage.

Individual Recognition

Clues as to the identity of the communicator are present in some of the vocalizations such as the RRV; they may be present in some others, but no basis for this has yet been established. Many features of the context must also work to aid in characterizing individuals, including peculiarities in plumage, phlegmatic or nervous dispositions, location of territory, and association with another individual. It is difficult to imagine how the social organization of the Eastern Kingbird could function without individual recognition. Birds who could not recognize their mates or offspring would become involved in much more aggression, males who could not recognize their neighbors individually would have constantly to reaffirm territorial boundaries, and environmental monitoring (see below) would be much more difficult. All of the other problems that must be met would be vastly more complicated in the absence of individual recognition.

Unequivocal evidence that kingbirds do recognize one another individually is not easily obtained, for one should have to know that a given encounter would have been different had the birds acted with or without this information. The best evidence is probably the behavior of two kingbirds during pair bonding. At first the male treats the female very aggressively, yet as she persists in associating with him his reactions change, and he soon comes to accept her. Toward all other kingbirds, however, he remains in most instances quite aggressive.

Appeasement and Reassurance

Since all adult Eastern Kingbirds look alike, and since males attempt to exclude other males from their territories, there often arise situations in which an excited male attacks his mate. She rarely fights back in such cases, and if, for example, she is flying to her nest, she will continue there while exchanging displays with her mate. Such "mistaken" attacks are particularly common early in the period of pair formation and become quite rare after the first few days, although they never disappear. There are also other causes of intra-pair aggression. For example, both individuals become easily provoked into aggression after the eggs hatch, and, while this aggression is primarily in defense of the young, it often carries the birds into momentary states in which they begin to fight with one another. Finally, when the fledglings have been out of the nest a couple of weeks, they, too, look very much like adult kingbirds, and they continue to persist in following (almost chasing at times) their parents, eventually eliciting aggressive responses.

None of this intra-pair or intra-familial aggression holds any advantages for kingbirds, and it has to be controlled. In most instances individual identities should be obvious to the birds, and this alone should act to damp the aggression. In fact, it is presumably because of individual recognition that most intra-pair encounters result in no aggression (and no displays) at all. Whenever some uncertainty exists in a situation, though, aggression is likely to develop unless the uncertainty can be forestalled. This is usually done by mutual displaying, the birds indicating on the one hand that they are not going to attack (reassurance) and, on the other, that they should not be put to flight (appeasement). Both give basically the same displays, the LHV (or very rarely the ILHV) with WFt, not orienting toward one another. Similarly, a fledgling which has elicited aggressive response from a parent will use the LHV with WFt. The two necessary meanings both come from displays signifying only an interference with a tendency to locomote, and heavy reliance must be placed on context. It is probably because all of the necessary elements of context have not yet been successfully established that the process of pair bonding does not proceed smoothly. Formation of the pair bond itself does not seem to be directly mediated by displays, but by such behavioral patterns as the persistent approaching of a male by a female. However, if a nest-site-showing display does in fact exist, then it might function directly in pair bonding.

Threat

This problem is opposed to that of appeasement and reassurance. Threat is necessary in a number of situations to underscore the tendency of the communicator to respond aggressively. The situations eliciting response are varied, and include the intrusion of a conspecific into the territory, the approach of a potential predator, the unwanted copulation attempt of a male, the approach of a male too close to a nest, and the persistent begging and following of a fledgling. Displays which can function as threats include: WFk, Tail Flick, Crouch, RCP, RRCP, Gape, Bill Snap, ILHV (perhaps), RV, CdV, harsh CV and harsh LHV. Some of these encode different degrees of aggression than others, and some encode a notion of ambiguity in addition to aggression. Several of the displays can be used simultaneously (as Crouch with WFk, Tail Flick, RCP, Gape, and a vocalization such as RV) and must result in a considerable amount of redundancy. Further, in a very aggressive individual it may be very difficult to identify the vocalization being used, because most of the vocalizations (ILHV, RV, harsh CV, CdV and harsh LHV) intergrade as they become harsher sounding and more frequently repeated. In fact, the most common sort of intermediate vocalization in this species is one which results from the modifying effects of harshness and repetition. It seems as if any of the five vocalizations just mentioned become less distinct in the process of being made more and more harsh until they lose their former identity (this will be discussed further in a subsequent chapter).

In some cases threat and appeasement/reassurance are not easily separable. When a female returning to her nest directs a CV to her mate, for instance, the effect may be sufficiently a defensive threat that the appeasement/reassurance functions are achieved simultaneously.

Environmental Monitoring

The previous two problems have involved birds as they have encountered one another. As in the case of advertising, however, much communication functions between individuals not in each other's immediate presence. In fact, a major function of communication must be to enable other conspecific individuals to monitor the environment. The rate at which a male, foraging in his territory, vocalizes, and the vocalizations he uses (say, RV, ILHV, or CdV), must provide his mate, setting on the nest, with some clues about the situations he is encountering. It should also provide his neighbors with like news.

Females apparently make use of such a system of monitoring by not coming off the nest at times when their mate is calling excitedly. In addition, it is possible that some of the vocalizations are used at times when they enable the members of a pair to coordinate their movements better, so that the nest is more continuously guarded.

A sample of 56 observations made of five different incubating females showed that on 82% of the times they left the nest to forage at a distance their mates were present on guard perches, usually commanding a clear view both of the nest and the sky around. Probably at least two factors are operative here: a tendency of female kingbirds to remain on their eggs when their mate is not nearby, and a tendency of the males to return periodically to perches near the nest to feed, to rest and preen, or to guard. Males do appear to have a tendency to come back from peripheral foraging areas to the nest vicinity at irregular intervals of about five to 20 minutes (although how often any particular male returns may depend in part not only on individual differences between males, but on such features as the number of suitable perch sites in the nest area. A suitable perch site is one that can be used both for guarding and foraging, and if there are several trees the male is likely to spend more time near the nest than if there are few).

The females have a cycle of incubating and foraging, and the problem is to bring this cycle more or less into phase with the central-peripheral cycle of movements of their mates. This could be done by having the female adjust her cycle, and leave the nest only when her mate is present on a guard perch if he returns sufficiently frequently. Females probably do make such an adjustment. Occasionally a female will quit her nest when her mate is not near, and will stay off only briefly and in the immediate vicinity, suggesting a reluctance to leave the nest unattended. Apparently, though, such a system does not operate during about 18% of the departures of females from the nest to peripheral foraging areas.

A sample of 61 observations made on the same five females returning to their nests to incubate after a foraging absence revealed that their mates were present on guard perches on 56 (91%) of the occasions. That the males should be more often present when females return than when they leave might be due to (a) males discovering unattended nests on one of their periodic visits to the nest region and staying to guard, a possibility apparently confirmed at times by field observations, or to (b) a mechanism by which females let males learn that they have left the nest. This second possibility could be accomplished in two ways. *First*, the female could signal on leaving the nest if her mate were not present — and in some such cases a female will call, usually an LHV. *Second*, the male could indicate his location to the female, and she could simply fly close enough past him to attract his notice. At times she certainly does fly in his direction (although it will take a large number of careful observations to show that this happens more often than would be expected by having her choose that direction to go for foraging, particularly if both members of the pair tend to share a relatively few foraging sites). One might suppose that, in order to fly directly toward him from the nest, she would either have to be able to see him from the nest, or would have to have heard him call very recently. Males are usually perched high in exposed places, and can likely both see the female and be seen by her, although in many cases it is difficult for an observer to know just what either bird can see.

In the cases of at least some nests, there are certainly regions in which the male forages which place each bird out of sight of the other. I have observed a number of instances in which either the female called on leaving the nest and the male promptly came from some distant foraging area and took up a guard perch, or in which the female flew toward the male and he, in turn, flew up and came to a guard perch. In some of the latter instances it is quite possible that she learned his location by hearing him use the RV; in other instances that he had not been calling and she was likely able to see him when she left the nest. The possibility of vocalizations functioning to help correlate the male's guarding behavior with the female's need to be absent from the nest periodically to forage cannot be proved from the data at hand, but remains worthy of further research.

It should not be assumed that a kingbird is "guarding" simply because it is perched near the nest, even though the fact that one of the adults is almost always near the nest, without any other functional reason for being there in many cases, would suggest this interpretation. Since kingbirds usually do, however, chase or attempt to chase all potential predators from a region surrounding the nest, the term guarding does properly suggest the functional reason for perching in its vicinity. I have witnessed similar defense of the nest in many related tyrannids, and it has been reported frequently in the literature (e.g., Eckelberry, 1964 and Skutch, 1960). Nor are tyrannids the only passerines in which males guard the nest in the absence of their mates (for instance: Nice, 1937, pp. 126-129, describes nest relief and guarding by male Song Sparrows (*Melospiza melodia*), and Skutch, 1960, p. 262, mentions this habit in corvids).

It is necessary to say that kingbirds usually chase all predators away from the nest vicinity, for there are occasional lapses, and there are situations in which some hawks are customarily not harried. For instance, a pair of *T. vociferans* studied in Arizona had its nest within 100 yards of the nest of a pair of Cooper's Hawks (*Accipiter cooperii*). The hawks had begun to nest before the flycatchers arrived from their wintering grounds, and had apparently hatched young by the time the flycatchers began to build. Possibly the latter had habituated to the presence of the hawks, although they were not habituated to the appearance of the young, and when these fledged and perched in the local trees they were attacked persistently. In another case, Taylor (1946) describes a *T. forficatus* pair and a *Buteo jamaicensis* pair nesting in the same tree — neither apparently paying much attention to the other. Hawks have long been known to have neutral areas around their nests in which they do not hunt; perhaps this behavior functions to keep them from being persistently mobbed by allowing the local birds to habituate to their non-dangerous presence.

Alerting

This function of the displays should probably be considered as a special case of the monitoring function. Here the recipient is given information about a dangerous or potentially dangerous situation. The use of such displays as the CV or Crown Ruffled indicates only that an unresolved change in the environment perceived by the communicator is potentially troublesome. Persistent repetition of the ILHV, though, is in my experience characteristic of situations in which a kingbird is faced with the choice of attacking or not (as when I've presented a stuffed owl decoy) and is much inhibited from attacking. Similarly, use of the very harsh RV or Bill Snap can be heard by a bird which cannot see a fight, but which can thus learn that a fight is in progress. An incubating female, then, might learn that her mate is attacking something, but if she can't see whether this is a neighboring male or a predator, then she should probably remain on the nest. If harsh RV calls are followed by AeV, then a kingbird has lost a fight. If her mate has lost, then she might encounter considerable danger if she ventured out; if another kingbird lost to her mate, then her mate is probably still aggressive and might attack her. If the AeV came in a Tumble Flight by her mate, then the danger has been driven from the territory, but her mate may himself be highly aggressive, at least briefly. In any such case, the use of a display alerts the recipient to a potentially dangerous situation.

Parent-offspring Relationships

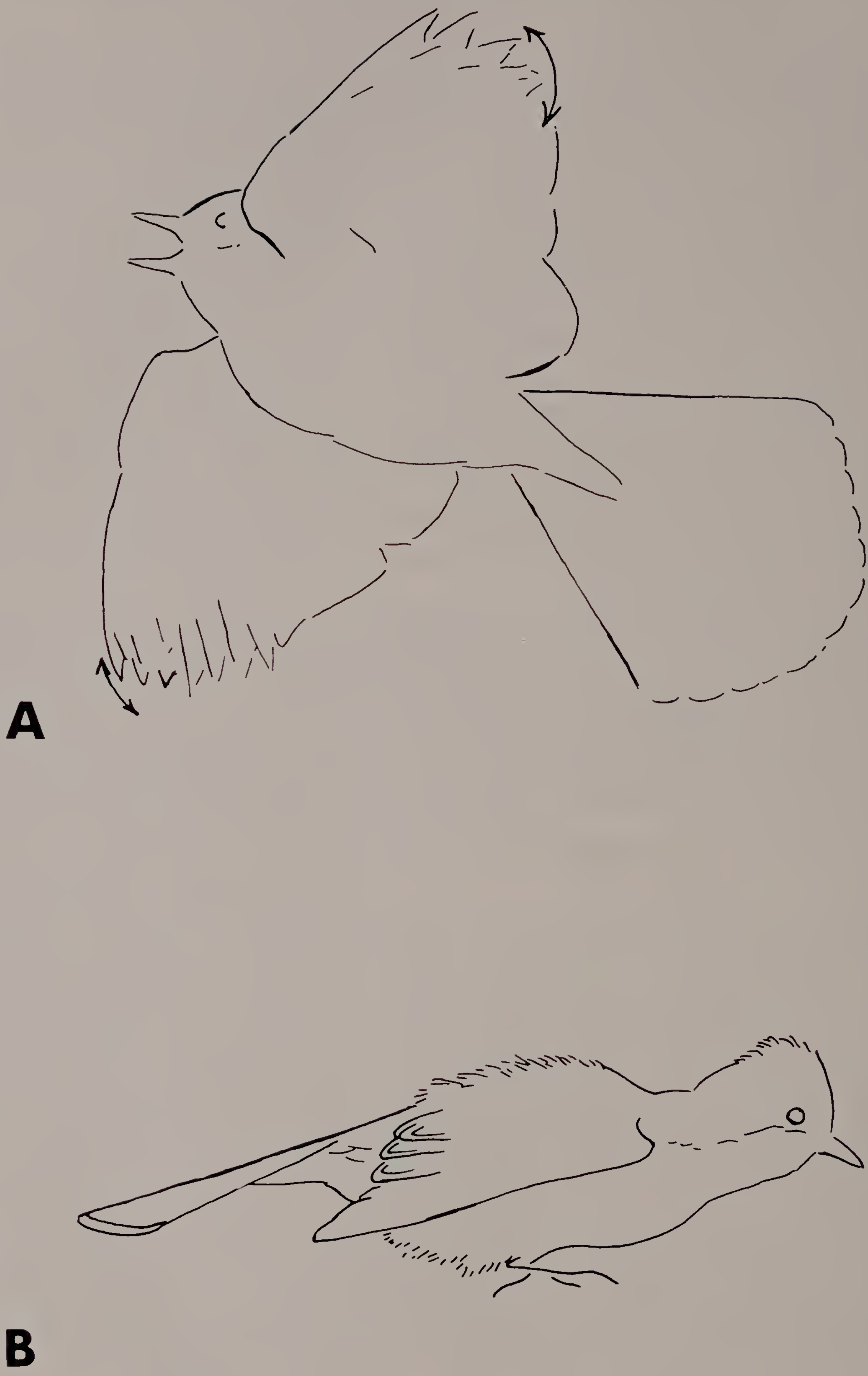
Kingbirds must face the problems of raising offspring, and displays are used in coping with these. The young can not only signal that they are hungry and have probably perceived a parent, but, once they have fledged, can identify themselves (at least to species) and give away their location. Marler (1956, p. 252) has described and similarly interpreted two vocalizations of young Chaffinches (*Fringilla coelebs*). The parents have no vocalizations which they direct to the young until the latter are becoming independent, and threat, appeasement, and reassurance become important.

The use of localizable calls by the fledglings brings up a special aspect of context — calls vary in the ease with which they can be located in space by a recipient equipped with two ears. The begging lisp of the nestlings is much less easily located than is the juvenile ILHV, and Marler (1955) has pointed out the logic of this. The parents, after all, know the location of the nest from which their offspring are calling, but there is good reason not to betray this location to predators. All of the adult calls of this species are quite easy to locate and, indeed, there is little reason for a bird which is made conspicuous by its mode of life to have a ventriloqual call, though some calls, such as the CV of a female in the nest, are notably faint.

The above account should indicate how the various displays, overlapping in message, meanings, usages and even at times form, can meet the necessary functions dictated by the problem of procreation and the social organization of the species. Not surprisingly, where communication must exist between distant individuals, the signals are primarily vocal, the quite conspicuous Tumble Flight, aided by its vocal accompaniment, being the one exception. At closer quarters, postural displays and plumage erection are important, and, particularly in the case of threat, these can express a graded series of probabilities. Yet even here vocalizations continue to be used and may even exceed the other displays in their importance. Indeed, the relatively invariable WFt which accompanies the intricate and highly modifiable LHV, gives the impression that in many cases the vocal display has such primacy that the postural accompaniment serves primarily as a background of sustained redundancy operating through a different sensory system of the recipient.

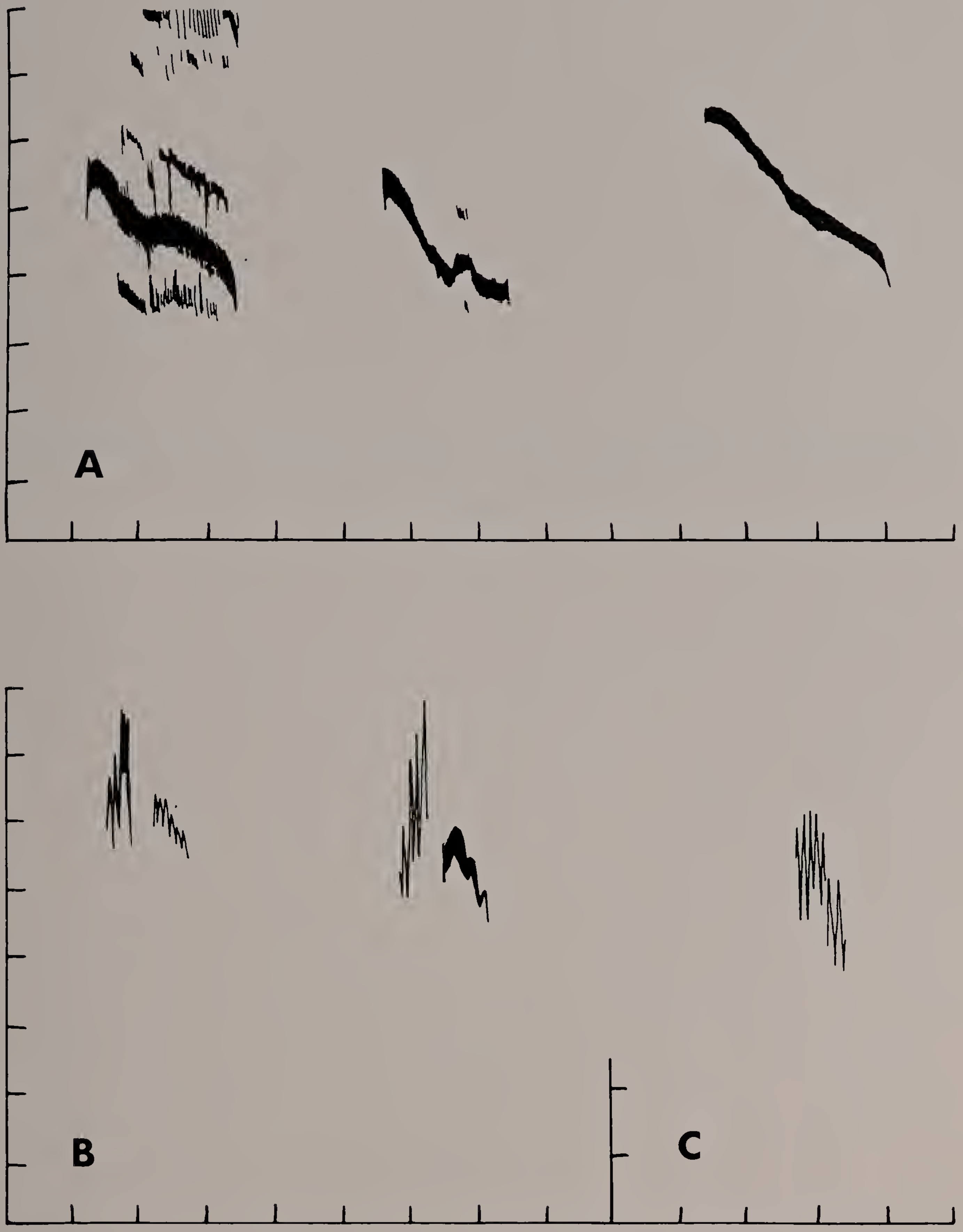
I am not convinced that the communication system of the Eastern Kingbird functions efficiently at all population densities, although I have not yet attempted to measure its efficiency (which would probably be a most difficult task). The lone New Hampshire male might have benefitted from the presence of neighbors stimulating him to display more frequently, and perhaps to make his RRV more regular. Nonetheless, he did obtain a mate each year, even though they failed to bring off a brood on the two years for which I have information. At Delta the population density may have been higher than the optimum. For several weeks at the start of the season there was a constant hubbub, males spent considerable time reacting to one another, and useful monitoring information probably got lost in the confusion. Pair bonding appeared to be difficult, and it took males a long time to accept females without reacting aggressively to them. Territories were not at all clear to me, and I doubt if they were to the birds. While this is probably typical of kingbirds and may usually be unimportant, it seemed to increase the number of birds per encounter and to be a factor in making pair bonding difficult. Conspecifics were at times tolerated in the same tree as the pair, and these invaders would often make persistent attempts to mount the female. Further, with the prolonged activity of the males there was extensive patrolling at the start of the season; this must have reduced the number of possible meanings that could accrue to this activity. Finally, in most of the pairs kept under observation, one or more nests were constructed before the nest which was finally used. These extra nests may have had a role in pair bonding, though they may also have been indicative of an unsettled state in the females which built them.

Figures



Tyrannus tyrannus

FIGURE 3:1a. Wing Flutter by a male calling LHV and following his mate as she returns to work on nest.
3:1b. Crouch display by male opposing a territorial intruder.



Tyrannus tyrannus

Figure 3:2a. Begging call of nestlings.
3:2b. ILHVs of a nestling and a fledgling.
3:2c. Harsh vocalization of a fledgling struggling to regain its balance.

DISPLAY BEHAVIOR OF OTHER SPECIES OF *TYRANNUS*

Chapter 4.

WESTERN NORTH AMERICAN SPECIES

Tyrannus verticalis, Western Kingbird

The Western Kingbird has a fairly pale gray head with a noticeable black mask extending from the bill through the eye and onto the ear coverts. Its chest is also pale gray, but its underparts are light yellow; the back is a light olive-green, and the wings are a fairly dark brownish-gray. The tail is nearly black with white outer margins, and is not notched. The patch concealed in the center of the crown feathers is orange or orange-red. The species breeds from the southern interior of British Columbia eastward to south central Manitoba, southward through the central United States to northern Texas and, farther west, to northern Mexico. It is migratory, wintering chiefly from western Mexico south along the drier side of Middle America to Nicaragua.

I first studied the species in 1960 at Delta, Manitoba, where its range has been expanding eastward and has overlapped the Eastern Kingbird's range since about the turn of the century. I studied it again in June and July of 1962 along the east side of the Chiricahua Mountains in southeastern Arizona, and briefly in adjacent New Mexico and west as far as the Rio Sonoita above Nogales, Arizona.

The life history of the Western Kingbird is similar to that of the Eastern (pers. obser. and Bent, 1942). Most individuals may be unmated upon arrival on the breeding grounds in spring, although an observation by H. A. Hochbaum (*pers. comm.*) indicates that some are probably paired when they arrive. Males quickly begin to stake out loosely defined territories, which they patrol and over which they fight. Within a little over a week after their arrival most of the birds at Delta seemed to be paired and in possession of sites. Males apparently have a nest-site-showing display like that of *T. tyrannus*, but females do all of the nest building, incubating and brooding; in most cases females also do most of the feeding of the nestlings, although some individual males are quite attentive.

Locomotory Hesitance Complex of Vocalizations

The usual pattern of the LHV of male *T. verticalis* is a series of elements in which there is an immediate decrease in frequency and then an increase back to the starting level within about the first dozen elements, the series sometimes being prolonged beyond this with no further frequency fluctuations (see fig. 4:1a, b). Almost all of the elements are arranged in couplets in which a relatively faint and low frequency element precedes a more emphasized, higher one. There is much variation, so that there may be more than one region of frequency fluctuation, the terminal portion may be dropped, all of the elements may be about equally emphasized, and a modified CV (q.v.) may be appended. Females rarely utter an LHV that much resembles this, although they may at times string together several ILHVs rapidly and with a frequency fluctuation similar to the beginning of the usual male form. Customarily the female form is much more brief — a pair of elements of greater duration than those which males use, and which sound rather like "kee-kee" (see fig. 4:1c). These elements have a tendency to develop a second peak, particularly when a female is calling more often than usual. Under some conditions the couplet is repeated one or more times in quick succession, but it is usually possible to detect the paired arrangement of elements within such a longer burst. Females also tend to lapse into CV calling, particularly around the nest.

When one member of a pair approaches its mate, both may use their different forms of the LHV along with the WFt. The situations in which this occurs, and the correlations between these situations and the different degrees to which the LHV is prolonged or abbreviated, closely resemble those of the comparable display in *T. tyrannus.* Further, a highly agitated individual of either sex may utter an LHV while landing, even if not in the presence of its mate. The display is sometimes used before or after fights, and may be unusually prolonged at such times. It may be used by males during patrolling as they approach landing sites with the WFt display, but I lack tape recordings of such instances with which to verify this. A call of the same general pattern as the LHV is sometimes used in these landings, but this could be the the Compound Repeated Vocalization (q.v.).

Incipient LHV

The vocalization that appears to correspond to the ILHV of *T. tyrannus* has two elements of which the second is brief and simply chevron-shaped, while the first is prolonged and rather variable (see fig. 4:2a). The form probably most common sounds something like "pwuh-T," while another version, in which the first element is slightly briefer and more rounded, sounds more like "pwee-T." The latter, especially, looks remarkably like a mirror image at lower frequency of the "T-zee" ILHV of *T. tyrannus,* and even more like a mirror image of a CdV component in *T. vociferans.* Other versions may have a more rasping first element, or a very brief one which seems to produce a form intermediate with the RV. The ILHV resembles the LHV in two ways: (a) its second element is of the same form as the elements of an LHV, and (b) it is a couplet, while the LHV is composed of couplets.

Birds of either sex may use the ILHV, although females do not commonly do so. A male will sometimes utter an ILHV after exchanging an LHV with his mate; he is also likely to scatter some ILHVs among the RVs and CdVs of his post-RRV calling or patrolling, or before a Tumble Flight. Either sex may use the call and forms intermediate between it and the RV or AtV while mobbing a potential predator near the nest, but the RV is the most common call in such cases. I have heard a female utter ILHVs while going to her nest as I watched, although a CV would be more usual in that situation. On the whole, its usage seems sufficiently similar to that of the ILHV of *T. tyrannus* to merit applying the same name.

Repeated Vocalization

The apparent RV of *T. verticalis* is a single, brief, chevron-shaped unit (fig. 4:2b) somewhat variable in frequency and duration. It is used by birds of either sex when disturbed by a predator near the nest; when I approached a nest, for instance, one or both adults might fly back and forth overhead, repeating the RV at irregular intervals. When they at times swing close past one another they may switch to a brief LHV, or give a doubled version of the RV in which the first element is of quite variable length (fig. 4:2c) and of different degrees of approximation to the initial element of an ILHV. At the start of pressing an attack, the first element will have progressively more frequency fluctuation, and then all calls may be replaced by an AtV (q.v.). Males use the RV at times when guarding near the nest, and use it a great deal in post-RRV calling and in the evening when going to roost. It is one of the calls used with Wing Flicking, and in fights within the pair.

Persistent use of the RV by a bird mobbing me as I approached a nest was usually followed by not only its mate but also its neighbors flying up and joining in the mobbing (and sometimes falling into fights with each other). In Arizona, where some pairs nested in yucca stands in very open, arid country and normally called rather little, it was clear that the birds that arrived quickly after I had been discovered by one bird must have been responding primarily to either the calls or the mobbing flight pattern (or both) of the bird rather than to their own discovery of my presence.

Attack Vocalization

In almost any situation in which a *T. verticalis* is behaving aggressively, a harsh vocalization is likely to be used. In attacks on a potential predator or on a conspecific, a quite brief buzzing call is used either singly or in bursts of up to about five to seven evenly spaced units (fig. 4:2d). This is accompanied by such displays as RCP, RRCP, Bill Snapping, WFk, and Crouch, and seems to be the principal form of the AtV. Variations, however, abound, and intermediates to the LHV, CdV, ILHV, CV, and even to the RRV are known. The last involves replacement of the ultimate elements of the main RRV phrase with

AtVs, and is not uncommon toward the end of morning calling; in the post-RRV period the CdRVs often gain similar harsh suffixes.

During the daily post-RRV period, males are even more prone than usual to get into fights with conspecifics, and so the frequent occurence of AtVs in their calling at this time probably does correlate with some sort of aggressive state. As in the RV, however, it is not clear that the calling males are aggressive, but only that they are easily made aggressive. The same holds true for the use of this call during patrolling when, for reasons I do not understand, harsh, buzzing calls are not uncommon during flights, but are not common when the birds are perched. At least at Delta, Manitoba, males not infrequently used short harsh calls when pursuing insects, and sometimes it was obvious that more of these calls were used if the prey proved elusive. As in similar cases involving *T. tyrannus*, it is tempting to postulate that the unsuccessful pursuit was causing a heightened state of aggressiveness, but there is as yet no evidence (such as a greater than expected amount of fighting immediately subsequent) to support this hypothesis.

No Attackee Vocalization has been tape recorded from *T. verticalis*, although I have at times heard calls that started harsh and turned clear during fights, from fleeing birds, and from a male who was chasing a grackle (a potential predator larger than himself).

Compound Vocalization (CdV)

The CdV comprises a series of elements on the same general pattern as the male LHV, and the two vocalizations sound so much alike that I did not distinguish between them in the field. There usually are differences, however, which the birds probably can distinguish. The LHV almost always comprises a series not of single elements, but of couplets in which the second of each couplet is emphasized and higher; the CdV comprises a series of single elements like the emphasized ones (fig. 4:3a). The elements of the CdV are thus, except in the region of frequency fluctuation, very like RVs. In addition, the CdV is apparently likely to have a more prolonged tail of nearly identical elements and the LHV more likely to reduce or drop this tail; the region of frequency fluctuation in a CdV may be reduced or, rarely, eliminated, but is likely to be expanded in an LHV. More tape recordings are needed to explore the degree of intermediacy between these two displays.

The CdV seems to be used as the equivalent of the CdV in *T. tyrannus*, but the two are not necessarily homologous; recall that in *T. verticalis* the RV itself has the simple chevron shape of the CV of the other species (fig. 2:4).

I have recorded the CdV from males which were perched and countercalling during the post-RRV period. It is common then, but so is the LHV, given from a perched position and sometimes without WFt;

I don't understand this situation yet, but suspect that the relatively high level of activity of males at this time may be responsible for the usage of the LHV. The CdV is also common in countercalling at other times, however, and was used by males who were guarding and patrolling. I have not recorded calls given by males landing with aWFt while patrolling, so do not know if CdV, LHV, or both occur then. I have also not recorded some of the calls heard without WFt in fights and before Tumble Flights. At any time, but particularly in the post-RRV calling, the CdV may terminate with one or two harsh AtVs, and is accompanied by much RV and ILHV. Each CdV is likely to be preceded by an RV and an ILHV, in that order, and is *not* under most circumstances accompanied by a WFt.

Chatter Vocalization

The vocalization used by female Western Kingbirds when somewhat disturbed while building their nest, or feeding nestlings, is a rambling series of faint, simple units which sounds rather plaintive. While in many ways similar to the comparable display in *T. tyrannus,* its units are relatively prolonged and tend to be much less peaked; when fairly loud they may be quite flat, but when fainter do peak (fig. 4:3b). The bill is opened very slightly when a CV is uttered. A few observations make it seem likely that males have a nest-site-showing display in which they use this vocalization.

The CV also occurs commonly in "greetings" of the pair members at or near the nest. A female is likely to substitute it for her form of the LHV while at the nest, but a male is much less likely. Males sometimes utter elaborate variations of the CV at such a time (see fig. 4:3c) and these may appear to intergrade with both LHV and AtV forms. The frequency modulation is rarely as extreme as in an AtV, but it occurs in varying degrees and is often very pronounced. When a clear and relatively emphasized unit precedes a series of shortening harsher units and is then followed by an ILHV, the over all form is suggestive of the first part of an LHV; the short units may even be grouped into couplets. Such series are among the most varied calls I have recorded. Accompanied by the WFt, they seem to replace the LHV at least at the nest, and this is comparable to cases in other *Tyrannus* species in which the CV may be used as a "greeting" under similar circumstances.

Regularly Repeated Vocalization

The form of this vocalization is similar to that of its homologue in *T. tyrannus,* following the same pattern of a stuttering introduction to a climax of high-pitched elements. There is an irregular and imprecise division into two or three phrases, the introductory ones comprising simple, chevron-shaped elements terminating in a similar, but emphasized, element of higher frequency. In the ultimate phrase a variable number of such elements precede the more elaborate and high-pitched section (fig. 4:4); then the final, brief element may repeat, and one or more of the repetitions may at times be harsh. The set of phrases is repeated, but with much variation except in the elaborated section, which seems to be fairly constant within any one individual. Examples recorded in Arizona and Manitoba are closely similar.

Most male Western Kingbirds repeat the set of phrases rapidly and regularly each morning of the breeding season, beginning in the predawn twilight. After about 15 to 30 minutes the display begins to break up, and the birds switch to typical countercalling or patrolling vocalizations, becoming usually only slightly less constantly vocal but much more active. The RRV is not customarily used during the day (for exceptions see under Tumble Flight), and does not recur in the evening twilight period of increased activity and calling.

Tumble Flight

In appearance this display is closely similar to the corresponding display of *T. tyrannus*, but it employs more elaborate vocalizations. Typically, as a *T. verticalis* ascends toward the point in the flight where it will twist, stall, and sometimes begin to tumble down, it utters bursts of vocalizations corresponding to the introductory phrases of the RRV (sometimes adding a few harsh AtV units, or AtV variants). At the point of making the sharp twist, which in this species may always precede tumbles, the bird begins the ultimate phrase of an RRV, then there is a burst of three to five staccato sounds, and the remainder of the RRV is completed either during the tumble, or even if no tumble is used. Recordings reveal that except for the staccato elements the vocalizations (fig. 4:5a) are exactly similar to the RRV — even to the point of having the number of ultimate elements vary from one to three. The staccato elements are added at just the right point to appear to represent the brief, repeated elements that are found in the complex RRV of *T. dominicensis* — that is, they make the vocalization appear to be a more complete RRV in a comparative sense. Yet the staccato elements are not vocal — they are the sound of a Wing Whirr, and the last of them sometimes overlaps with the succeeding vocal element.

In addition, I think that at Delta I sometimes observed Tumble Flights in which the vocalizations were less elaborate, apparently just the high-pitched elements; no case of this was tape recorded.

As in *T. tyrannus*, the display is most likely to occur during the daily crepuscular periods of heightened male activity when birds call much and apparently stimulate one another to perform this display. At Delta, even Eastern Kingbirds doing the display were likely to provoke Westerns into it, and *vice versa*, although in Arizona I did not see Tumble Flights by Cassin's Kingbird provoke Westerns to follow suit. In both species the part of the summer after the young had fledged and were persistently vocal became a time of much spacial intrusion by neighboring adults (possibly responding to the calls of the young) and was marked by an increase in the usage of the Tumble Flight.

In Arizona, where sites with fewer pairs than at Delta were studied and where individuals were in consequence more easily identified, I noted that by approaching the nest of one pair and being mobbed I often drew in the neighboring pair (or at least the male). In such cases the two males would usually interact, and one might do a set of tumbles and calls while flying toward the other. Usually the intruder began these, within the territory (not precisely defined) into which he was intruding. Both might then do the display flying in parallel, and once after an intruder had been chased back to his own area, he gave the full display once he had stopped fleeing — his opponent having turned back. In such cases I twice noted consistent differences between the two males in the vocalizations which they used; one would have one terminal element to the complex phrase, the other would have three.

At Delta I several times noted Tumble Flights by males of *T. verticalis* which had just chased potential predators from the nest region. In two such cases the male perched near the nest after the display and repeated the RRV, and neither case was in a crepuscular period. In at least two other cases the displaying bird finished the Tumble Flight and then without apparent provocation chased the nearest neighboring conspecific, which would indicate that he was quite aggressive. Usually after any Tumble Flight the bird that displayed would perch and call the RV frequently, with some ILHV.

Displays Using Wing and Tail Movements

Wing Flutter and Wing Flick. In the WFt the wings are partially extended laterally (fig. 4:6a) and fluttered rapidly through a small arc, apparently exactly as in *T. tyrannus.* The display is done by both birds of a pair as they utter the LHV or CV when greeting, and usually precedes a period of "acceptance" in which the birds associate together without agonistic behavior. Considering the close similarity between the LHV and the CdRV, the WFt may be extremely important in helping recipients distinguish between the two. The WFt also is used at times with agonistic behavior, however, as when it accompanies the Crouch posture. In such instances the displaying individuals usually appear "reluctant" to engage in more aggressive behavior, and may not further interact. To the extent that fighting does follow use of the WFt, the WFt becomes less frequent unless the birds are evenly matched—in which case it recurs between fights. I have a number of records of a male guarding during the time his mate was nest building, and using bursts of AtV (usually terminating with an ILHV with WFt; he sometimes approached but rarely attacked his mate when she came to the nest site, and he had several fights with a neighboring male in which neither used the WFt.

The WFk is also as in *T. tyrannus,* but is relatively rare. Either member of a pair may direct this display toward a bird of another species (e.g., a Baltimore Oriole, *Icterus galbula*) which ventures too close to their nest, and I have had a male vigorously direct WFks toward me when I was near a nest. When highly agitated by an agonistic situation the pair members may direct WFks toward one another. Occasionally displays are used which appear intermediate between WFt and WFk; sometimes the wings may be so little extended during a WFt that the carpals are not free of the body, or the wings may be raised over the back while fluttered (seen once, a female repulsing a copulation attempt).

Wing Whirr. Brief bursts of a noise probably produced by the wing tips, apparently just as in *T. tyrannus,* are sometimes used by males in fights. It seems to be a rare display, and I have only one set of observations, an intraspecific fight in which it recurred many times, and in which I could distinguish each time which male was using it. This encounter took place early in the season (17 May) at Delta and probably involved two neighboring males. At first they were nearly evenly matched, and did much Crouch posturing with WFt and highly varied CVs, rarely directly facing or actually fighting. Both did a great deal of bill wiping at this stage, although not later; this does not seem to be a ritualized activity, but must have signal value. Gradually, however, one began to dominate, used more RV, less WFt, and almost no CV (which the other continued to use) and pressed the attack much more frequently, using Wing Whirrs as he attacked. The losing individual fled after each encounter, but for a long time he did not flee far, and quickly circled back to renew posturing near the other bird. The loser did not use the Wing Whirr in any of the fights, but several times did as he circled back. Even though he was losing, he must have been highly aggressive to keep returning, and the fact that he used the AtV often just after breaking off from a fight tends to support this, as I know of no other case in which a bird using this vocalization gave any indication of being predominantly fearful. Thus both birds apparently used the Wing Whirr when sufficiently aggressive to approach their opponent. On another occasion I have known this display to be used with Bill Snapping by a male chasing an oriole from his nesting tree.

As mentioned under Tumble Flight, there is a second usage of the Wing Whirr display in *T. verticalis,* and that is at the point of twisting and beginning to tumble in the aerial display. The Tumble Flight, however, apparently has a message encoding a fairly high probability of aggression; when the Wing Whirr is used in the tumbles, the usage is consistent with that in actual fights.

Tail Quiver and Tail Flick. A Tail Quiver with WFt and a Tail Flick with WFk occur as in *T. tyrannus.* The Quiver may also occur without WFt during CV calling, and Tail Flicks at times occur with emphatic RVs and in CdV calling. In both displays, but most noticeably in the Tail Flick, the tail is at least partially spread.

Crouch

Use of the Crouch seems to be relatively rare as compared with *T. tyrannus,* but the exaggerated pose (fig. 4:6b) is quite similar. Usually there is less plumage erection, though, and the WFk is incorporated less often than the WFt. The partially spread tail exhibits broad white margins on its outer rectrices, but is usually flicked only during WFk.

As in *T. tyrannus* this display is used in encounters between two males, and often alternated with periods of fighting. At least early in the season, in addition, pair members also Crouch with WFt during greetings. They orient themselves so that they are not directly facing, and sometimes do not extend the neck (although sometimes I think they do). Later in the season their WFt comes to be given from a more upright stance on most occasions, although a bird may still occasionally Crouch or lean slightly forward and give a few Tail Flicks.

When Crouched with WFt during greetings the LHV is the usual vocalization, although the CV is often used. Highly variable CVs are also used by Wing Fluttering males Crouching before a fight, but are replaced by RV and AtV when the encounter becomes more active.

Revealed Crown Patch and Raised RCP

The orange to orange-red central patch of crown feathers of *T. verticalis* can be exposed, or, more rarely, raised. The displays are used by birds which are about to attack, are attacking, or are chasing. The RCP may even be used by the victor after a fight. It is not only much the more common display, but is perhaps relatively more common than its homologue in *T. tyrannus.*

Crown Ruffled and Other Plumage Signals

A fluffing or ruffling of the crown feathers, without parting them to expose the bright patch, is as common as in *T. tyrannus.* The throat is sometimes ruffled in agonistic situations, and a general fluffing of all body feathers occurs at least occasionally, but I am not certain what circumstances delimit it, and I think it may not be ritualized. Other plumage erection occurs in the Crouch posture, as in *T. tyrannus.*

Gape and Bill Snap

Gaping sometimes precedes attacks, but seems fairly rare. Bill Snapping follows Gaping or occurs in attacks without previous Gaping; it is common.

Displays of Nestlings and Fledglings

The young have a wheezing call used both in the nest and after they have fledged. It varies from about 0.2 to 0.3 seconds in length, and is highly variable in form; typically it peaks in about the first third of its length and then descends (fig. 4:5b). It is repeated rapidly when young are begging from a parent, and sometimes repeated, more slowly, even in the absence of the adults.

While still nestlings, the young develop a brief note (fig. 4:5c) which is abrupt but without a sharp peak. By the time they fledge it has apparently given rise to an RV and perhaps contributed to an ILHV, both slightly shorter than the usual adult versions. The fledglings tend to be fairly quiet in the absence of their parents for the first few days, and give only occasional versions of their RV. When thoroughly agitated, however, which happens if their parents become upset and begin chasing all birds away from the vicinity of the fledglings, the young will use (at least in flight) the AtV.

TYRANNUS VOCIFERANS, CASSIN'S KINGBIRD

This species is a dark olive-gray on the head, chest and back, and is thus much darker in appearance than the similar Western Kingbird. The throat is white and the underparts yellow, the wings and tail a dark brownish-black, and the concealed crown patch orange-red. The tail has a very narrow, inconspicuous light tip. Cassin's Kingbird breeds in the subarid southwestern states, and south through subarid portions of Mexico into Guatemala; its northern populations are migratory.

I studied the species from 31 May until 5 July, 1962, in and around the Chiricahua Mountains of southeastern Arizona, mostly at the Southwestern Research Station and the townsite of Portal. Some observations were made 15 and 16 miles north of Nogales, Arizona, in the valley of the Rio Sonoita on 18 and 19 June, 1962. In the early afternoon of 13 August, 1964, my wife and I made a brief set of observations on a family of adults and fledglings in eastern Mexico, about 41 miles north of Matehuela along Highway 57, in the state of Nuevo Leon.

Locomotory Hesitance Complex of Vocalizations

The LHV of *T. vociferans* males is a series of two-element units (fig. 4:7a) each of which sounds like "ch-tuur" or "ch-teer;" superficially, the vocalization is reminiscent of the "kt-ter" of *T. tyrannus*, although much lower pitched. The more prolonged second element of each unit can vary in the frequency to which it rises in peaking (or sometimes scarcely peak at all), in length, and in number of peaks. The first element is rarely omitted. Features by which this vocalization can be distinguished from the CdV are discussed under the latter.

While the male LHV of this species resembles that of male *T. ver-*

ticalis in having units comprising two elements, the first of which is less prominent than the second, the female LHVs of the two species are more comparable in form. A female *T. vociferans* does not usually utter her LHV units in couplets, but each unit is longer than, and of the same general shape as, the unit in the other species (see fig. 4:7b) and also tends at times to form two quite prominent peaks. Occasionally a form with one primary peak at the start will have three or more lesser peaks, much as in a similar variation of the male LHV.

The LHV is used with a WFt and tail spread in greetings between members of a pair. I have known a male to use it in approaching his mate prior to copulation, and again after dismounting. As in the few copulations I have seen in other species of flycatchers, the female gave no particular display, merely crouched slightly; the male gave a few harsh calls and bit the back of her neck just prior to dismounting. Males almost invariably use the LHV in the early, ascending portion of a Tumble Flight. They may use it in flight during patrolling (again, with a WFt) and sometimes even when perched and without a WFt during postdawn calling if they are particularly active and moving about frequently. Females use the call on leaving the nest if they are agonistically upset, and a guarding male, if present in such a circumstance, may fly after his mate uttering an LHV, then return to his guard perch. In most respects, then, it is a typical LHV.

The multi-peaked variants (fig. 4:7c) tend to be used by both members of a pair in situations when one, or usually both, is agonistically upset and behaving in a very agitated fashion. Sometimes the relatively slow frequency modulation of these peaks is audible even to a human observer, and the call seems slightly trilled. Usually there is considerable emphasis of two or more resonance harmonics above the standard ones in such cases.

Compound Vocalization

As in *T. verticalis,* males have a CdV (fig. 4:8a) in form very similar to their LHV. Intermediates exist in a number of situations, but the two vocalizations can usually be distinguished by the following characteristics: first, the frequency of the resonance fundamental, and hence of the higher harmonics, is slightly lower than in the LHV, and second, in the LHV the greatest emphasis is on the fundamental and nearly as much is placed on the second harmonic (and sometimes on several harmonics), and in the CdV the fundamental is quite faint and emphasis is placed *only* on the second harmonic. The net effect of these two differences is to make the LHV sound higher pitched and shriller than the CdV.

The CdV occurs mainly during patrolling and countercalling by males, particularly if they are moving about fairly frequently. In birds that are very active it is often the principal vocalization used in post-

RRV calling, although these birds sometimes use mainly LHV — even when perched, and without WFt. They do call in most of their flights, however, using LHV with WFt; possibly the high level of locomotory activity leads to the use of the LHV when perched. When countercalling, even such active individuals usually switch to either CdV or CdV/LHV intermediates. Such intermediates may have harmonic emphasis of the CdV sort with an intermediate frequency level. On the whole, though, a perched bird during patrolling or countercalling is much more likely to use CdV than LHV.

Intermediates between CdV and LHV also occur occasionally in the initial phases of Tumble Flights; in my experience these have all been of the multi-peaked form. In all such cases which I have recorded, the displaying male was not only very agitated, but appeared confused or perhaps anxious. Once I recorded from a female a string of units which appeared to be her LHV form with a fairly high initial peak and an incipient second peak; these units were given with the CdV harmonic and frequency characteristics and suggest an intermediate between the CdV and the female LHV. She gave this vocalization as a greeting in response to her highly agitated, rather aggressive mate.

Finally, one morning I heard a faint, mumbled form of the CdV which sounded like "kuh ruhr, kuhruhr-kuhruhr-kuhruhr" rapidly repeated over and over again for several minutes through closed bill by an individual which had intruded into a territory and was perched a few feet above the nest on which the female was setting. This ended when her mate arrived and chased the intruder away; I did not have my tape-recorder with me. Miller (1962) may have heard a similar vocalization regularly at midday from a relaxed-looking bird in its nesting tree; he describes it as a "faint whisper song," not like the RRV, but musical — a characteristic of none of the *T. vociferans* calls I have heard.

Repeated Hesitance Vocalization

T. vociferans does not seem to have a call that corresponds sufficiently closely to the ILHV of *T. tyrannus* to be given the same name. Rather, it seems to have two intergrading forms of Repeated Vocalization, both of which have some RV and ILHV usage characteristics, and other, to some degree overlapping, RV usage characteristics. The first of these may be called the RHV. It sounds like "tch-wEEer" and comprises two distinct elements, the first brief and explosive and the second prolonged, arched upward in frequency, and rather harsh (fig. 4:8b). Except in the harshness of the prolonged element, it closely resembles a unit of the male LHV.

Male Cassin's Kingbirds utter this vocalization when guarding and sometimes when patrolling. It is the most common vocalization in countercalling, and is common in post-RRV calling when it is often prefixed to a CdV, and may occasionally form intermediates with a CdV. It is sometimes used before or after the LHVs in greetings, and either male or female sometimes substitutes this call (or a harsh form of it) for the LHV in a greeting. Harsh forms of it are common after fights. It almost invariably precedes a Tumble Flight. In late evening, males may call it from their roosting sites if disturbed.

Simple Repeated Hesitance Vocalization

The SRHV is usually a harsh "rrEurrrr" of varying length; probably its most usual form (fig. 4:8c) is about as long as the second element of a standard RHV. Sometimes it is twice as prolonged, at other times it is shortened and intermediate with a harsh CV, and sometimes it is of its standard length but much less harsh, and appears very similar to the second element of the male LHV/CdV intermediate, or the terminal element of the first phrase of the RRV. Strings of this last clear form often precede the phrase two of the RRV when the latter is used in post-RRV countercalling, and occasionally (perhaps particularly in the case of females) may substitute for an LHV in greetings. By calling this form "simple" I mean to indicate that it has only one element; all possible intermediates are formed with the RHV, however, and the "tch" element is sometimes incorporated into an SRHV. On the whole, the SRHV is much less common than the RHV, and in this way more comparable to the ILHV of *T. tyrannus*. Other than in the post-RRV period it is not much used in countercalling, and it is common in guarding only if the calling individual is aggressively aroused. Occasionally it is used immediately before a Tumble Flight, and it is not unusual as a call prefixed to the CdV, although the RHV is more common there.

I am not sure that anything in the repertoire of *T. vociferans* can properly be viewed as an Attack Vocalization. Quite harsh vocalizations occur in several recorded fights and chases. These are sometimes abbreviated RHVs or occasionally SRHVs (i.e., RHVs without the initial "tch" element), sometimes apparently bursts of harsh, brief CV elements, and sometimes more prolonged harsh calls. The last may be lengthened CV elements; however, they are often about the length of a second element of a male LHV unit and, like it, it is often possible to recognize an internal fluctuation in amplitude and in frequency, leading to three or more peaks. The resemblance to a harshened LHV is heightened by the facts that (a) they sometimes occur in the early part of a Tumble Flight (fig. 4:8d) and (b) in an encounter between mates the female may use her LHV when the male uses this call. Thus all of the known harsh calls can be assigned loosely to some category other than AtV; all could be intermediates between the AtV and other calls, but the form of any possible AtV remains unknown.

Chatter Vocalization

I never heard a female Cassin's Kingbird utter at a nest any call that I felt was a CV; on the other hand, in the first few days of my observations (up until 2 June) I did hear a male use CVs away from the nest on rare occasions. This bird would behave as if he was nest site prospecting, but his mate already had a nest, and probably a clutch. He would move slowly about in a bush and repeat a prolonged set of fairly low pitched, varied units sounding like "tuh" and which were of different lengths. The usual form appeared to be a couplet composed of a relatively prolonged unit followed by a very brief, louder unit (fig. 4:9a). Sometimes the long unit was simple, and sometimes it appeared to be compounded of rapid but fairly slight frequency fluctuations as if it was a version of the harsh, prolonged SRHV. The male sometimes did use what must have been bits of that harsh call in flight when he was agonistically upset — during fights or after a Tumble Flight. Once in a greeting between an agitated, aggressive male and his mate the mate used primarily a chatter comprising at first a string of fairly prolonged, low pitched nasal units between which she quickly began to insert the brief, loud units, forming the usual couplets.

It seems unlikely that females do not have a CV they use when anxious at the nest, and it may be only that they use it rarely; I did not watch the initial stages of nest building in any case.

Regularly Repeated Vocalization

The RRV of *T. vociferans* is the most rasping of any of the kingbirds' calls. It is rather variable, but usually comprises two distinct phrases. The first phrase, occasionally omitted, has one or two rasping elements followed by a more prolonged "keeeyur" (which is the clear form of the SRHV). The second and more complex phrase begins with a rasping element, which is succeeded by one (sometimes two) very brief elements and a second rasp ascending in pitch; then come two clear and more or less chevron-shaped elements and an odd rasp which is frequency and amplitude modulated. Usually there is an additional element on the end; it is usually harsh (as in fig. 4:10a) but sometimes clear. Cassin's Kingbirds in the Chiricahuas and farther west along the Rio Sonoita above Nogales all used quite similar forms of the RRV. Within my sample, the variation of any one individual seems as great as the variation among individuals, but a larger sample might reveal consistent inter-individual differences.

As is the case in other kingbirds, this RRV is used beginning early in the predawn twilight and continues in a roughly regular form until shortly before sunrise. While camped by the Rio Sonoita during a time of full moon, which rose above the side of the valley about 10 p.m.

the birds of that dense population used the call intermittently from 12:30 a.m. through the remainder of the bright night and on into the usual predawn chorus. Series of "keeeyur" elements were common at first, and took the place of first phrases. Pauses between bursts of RRV calling became shorter and shorter until about 0300 when the first bird began continuous alternation; others took it up, and calling was continuous until at least 0450. At other times of day the RRV can be heard, at least briefly, at any time there is a thunderstorm. Rains began at the end of June in the Chiricahuas in 1962, and in the dark, cool periods around each storm the Cassin's Kingbirds often uttered RRVs and did Tumble Flights.

In this species the RRV is also an important call in the period after the fairly regular predawn calling, and its use often extends several hours into the morning. This did not happen for the first couple of weeks at one of my sites where relatively few pairs interacted and males patrolled actively over large areas; they tended to use primarily CdV, usually preceded by many RHVs, or occasionally by SRHVs. Around the Portal townsite, however, the population was dense, and males seemed to do much less active patrolling. Rather, they stayed in their roost tree or on some favorite guard station and countercalled. This countercalling had frequent second phrases of the RRV interspersed with series of "keeeyur" elements; often the latter were preceded by one or two brief harsh elements, or even by a very prolonged harsh SRHV — that is, they appeared to be modified first phrases. Occasionally the "keeeyur" elements might be replaced by an RHV, but this was uncommon unless the birds began to be active and to have encounters. In the latter case, the second RRV phrase usually was dropped, and more CdVs appeared. Similar countercalling sometimes took place in the late evening twilight, and some quite regular and sustained RRV usage was recorded (e.g., fig. 4:10b) on a few evenings.

Some usage of the RRV in situations similar to the above at times of day other than the morning twilight has been recorded in several other species, but it was unusual in all cases except *T. dominicensis*, the only other species I have known to sing at night, long before nautical twilight.

Tumble Flight

In its full form the Tumble Flight of *T. vociferans* looks much like the corresponding display in *T. tyrannus*. The displaying individual makes an ascending flight, calling most of the time, then stalls, pitches forward or twists and pitches, and tumbles down for five feet or more as if grappling with an unseen opponent. In the ascending flight the usual calls are RHVs, although sometimes they are long, harsh SRHVs, or modified LHVs. Beginning at the point of stalling, whether there is a subsequent tumble or not, the bird utters a complex vocalization which is a slightly modified second phrase of the RRV. The first harsh element and its subsequent brief note are apparently compressed into one, brief, harsh element (fig. 4:9b), and then comes the ascending harsh element. The two clear elements are not used, but are replaced by a prolonged Wing Whirr often extending beyond the final vocal portion. The odd harsh vocal element with varying frequency and amplitude is used, but it is more prolonged, the additional part being at its onset, so that it follows quickly upon the previous harsh element and takes up the position the two clear elements would have occupied in an RRV phrase. This is followed by one or two very brief harsh elements.

The close similarity in form between this Tumble Flight vocalization in *T. vociferans* and the form used by *T. verticalis* is remarkable for its detail. In both species the second RRV phrase is used in a slightly modified form. In *T. verticalis* the phrase lacks certain brief elements that are found in some other kingbirds, and these are "replaced" by the staccato sounds of the Wing Whirr. *T. vociferans* does not lack elements in this position in the RRV phrase, but they are not extremely brief, and are eliminated in the form used in the Tumble Flight. The gap is covered vocally by extending forward the subsequent element, and this species also gives a burst of Wing Whirr.

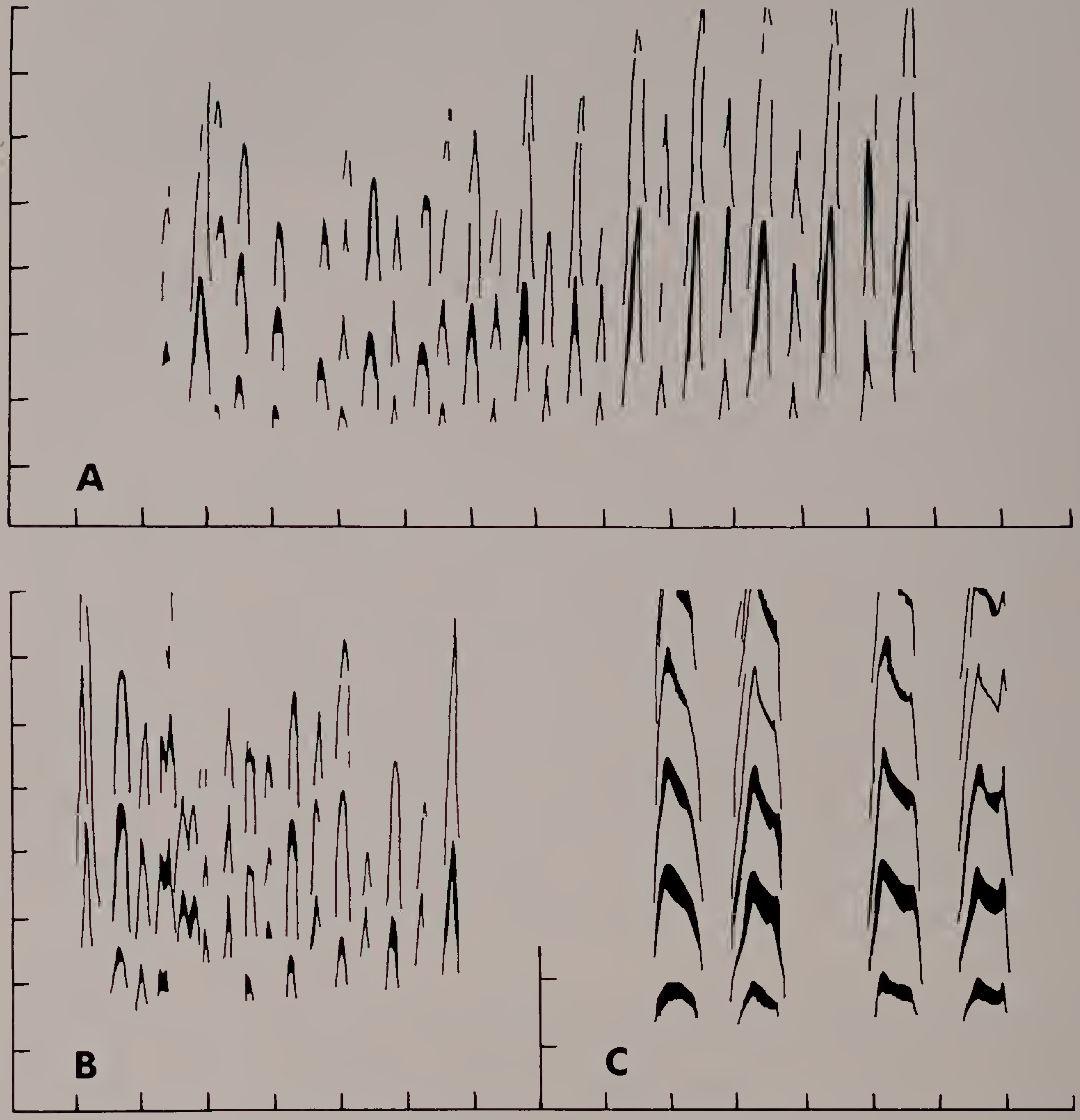
Males use Tumble Flights during morning and evening countercalling fairly frequently. Once I saw two males fly up and proceed on parallel courses, both using the display. The display is not common at mid-day except in the dark intervals around thunderstorms once the rainy season begins. Occasionally a highly agitated bird performs a display with modified LHVs and very incomplete phrases and no tumbles; full tumbles are not, in fact, common, but twists are nearly invariable, and slight tumbles fairly common.

Non-vocal Displays

Both mates commonly use a Wing Flutter when greeting with LHVs, either in flight or when perched. The display is much like the WFt of *T. tyrannus,* although the wings are usually held just slightly over the back; the tail is always spread, but I did not see it being quivered. WFts also accompany other uses of the LHV, and the apparently unritualized hesitant flight also occurs at times, when a bird is behaving as if confused, as before and after some of the aberrant Tumble Flights which were seen. I have not seen Wing Flicking although Tail Flicking accompanies advanced forms of the Crouch posture. The latter also seems typical — in full form the displaying individual adopts a nearly horizontal pose, extends the neck and points the bill downward slightly, while freeing the wrists and sometimes drooping the wing tips. The full form is seen when two birds are having a standoff agonistic encounter and are displaying toward one another from close perches, not directly facing. Less complete versions are seen, as when a pair greets after the male has been actively chasing and fighting with his neighbors; both mates will crouch at least slightly, while using the WFt and LHVs.

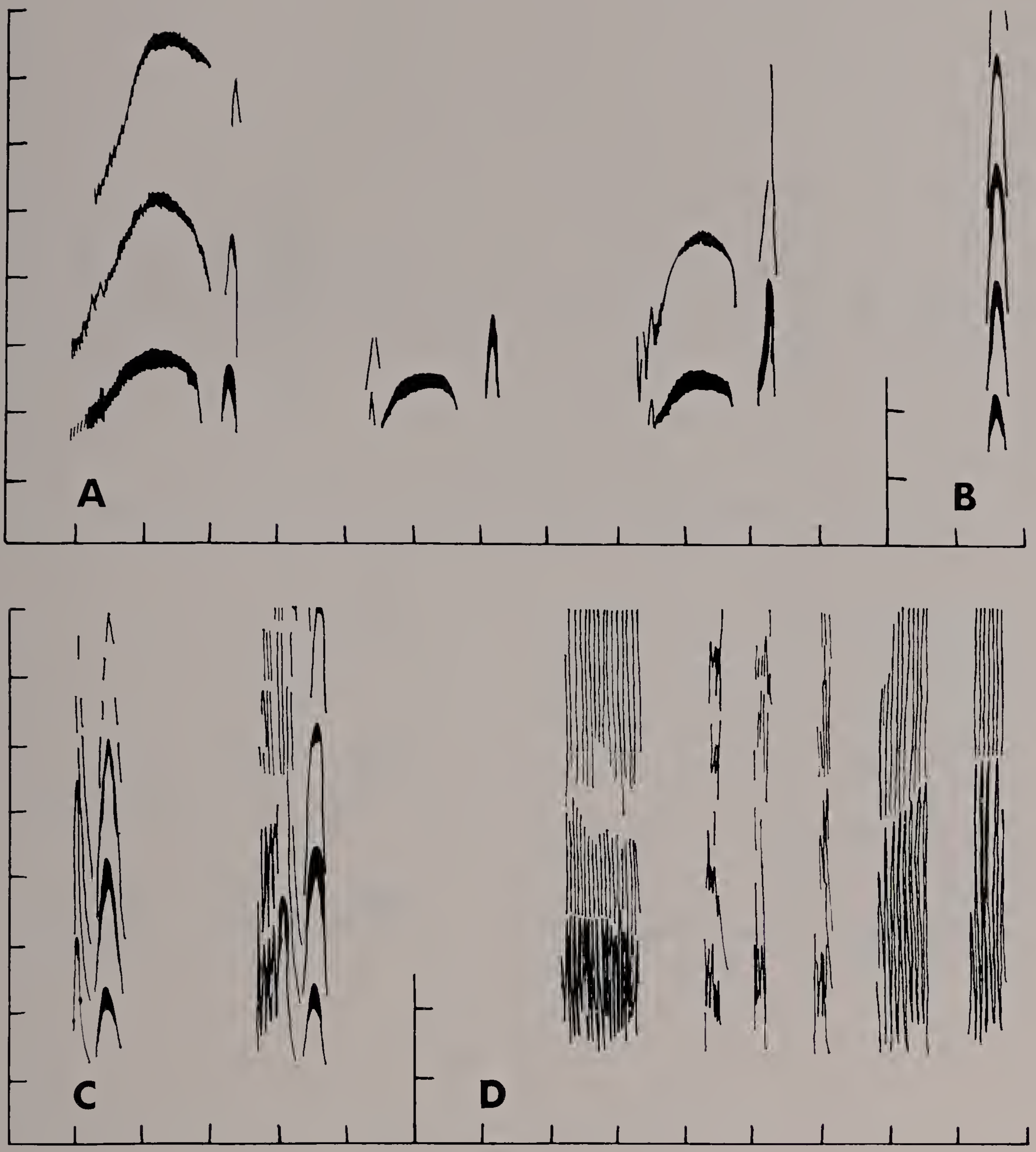
A Wing Whirr is known in Tumble Flights, and also occurs in violent chase/fight encounters, when both combatants may use it frequently in flight; it is particularly noticeable when they are making sharp turns and twists. Bill Snaps also occur in these fights, along with actual biting, some harsh, brief vocalizations, and some long harsh SRHVs. I have noted no other non-vocal displays, but the species probably uses its crown patch in RCP and RRCP displays.

Figures



Tyrannus verticalis

FIGURE 4:1a. LHV of male greeting mate near nest (her call not shown).
4:1b. Shorter LHV of same male greeting mate (her call not shown).
4:1c. Two couplets of female LHV greeting mate (his call not shown).



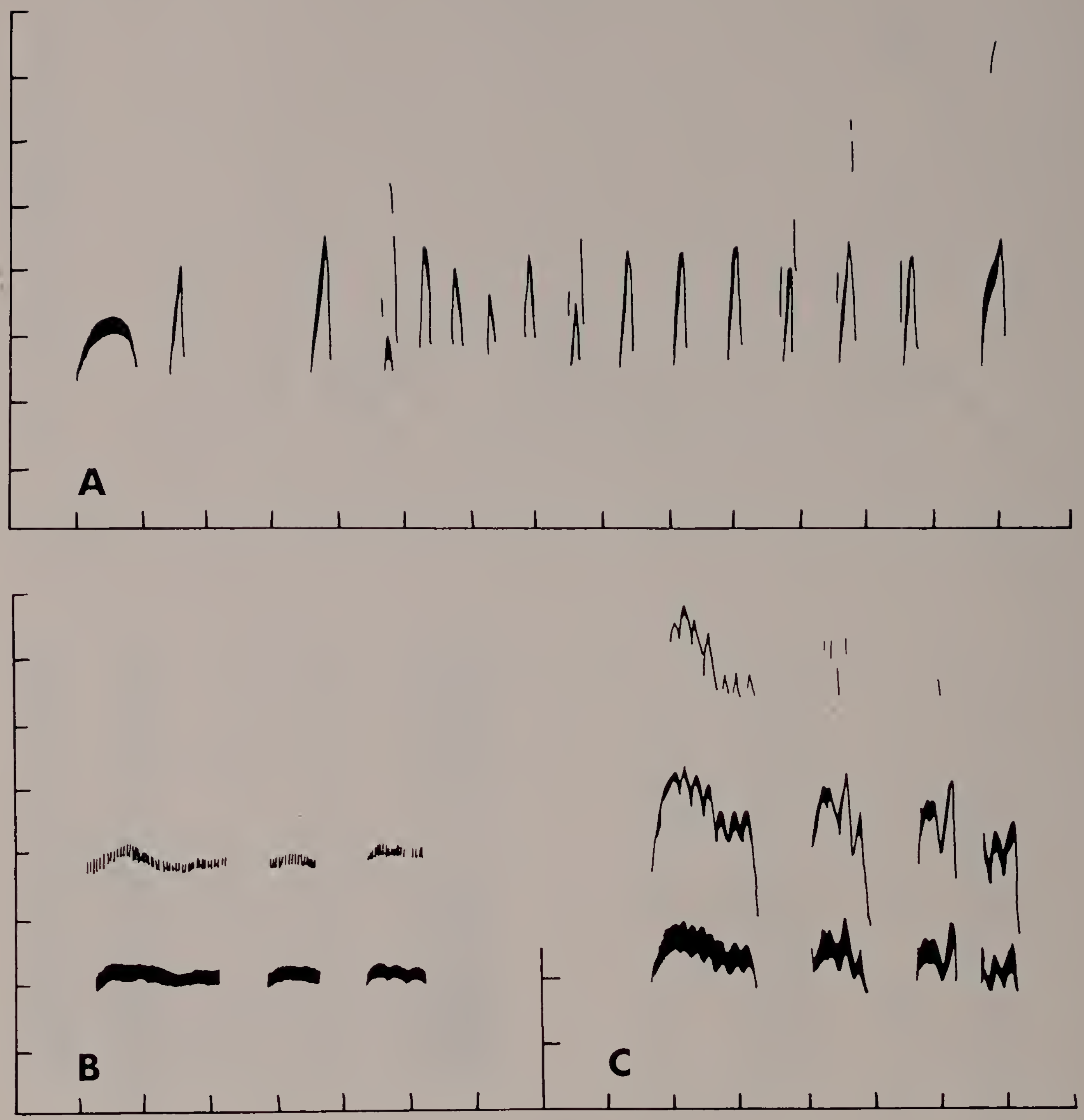
Tyrannus verticalis

FIGURE 4:2a. Three examples of ILHV, not in sequence (second two were by a flying bird).

4:2b. RV by a bird near nest, disturbed by approaching human.

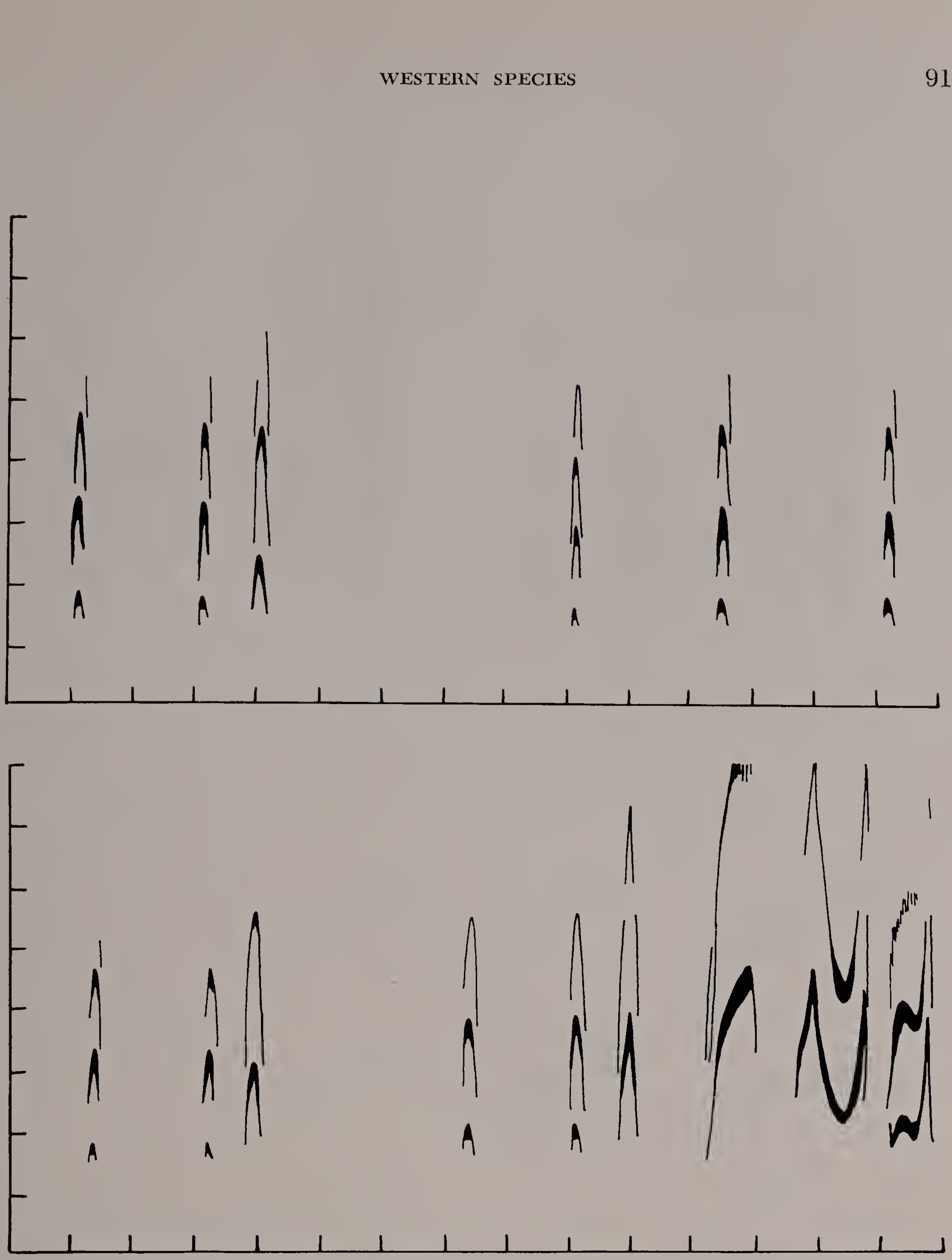
4:2c. Two "doubled" RVs by this bird flying over head (not in sequence).

4:2d. Burst of AtVs by this same bird, approaching recorder.



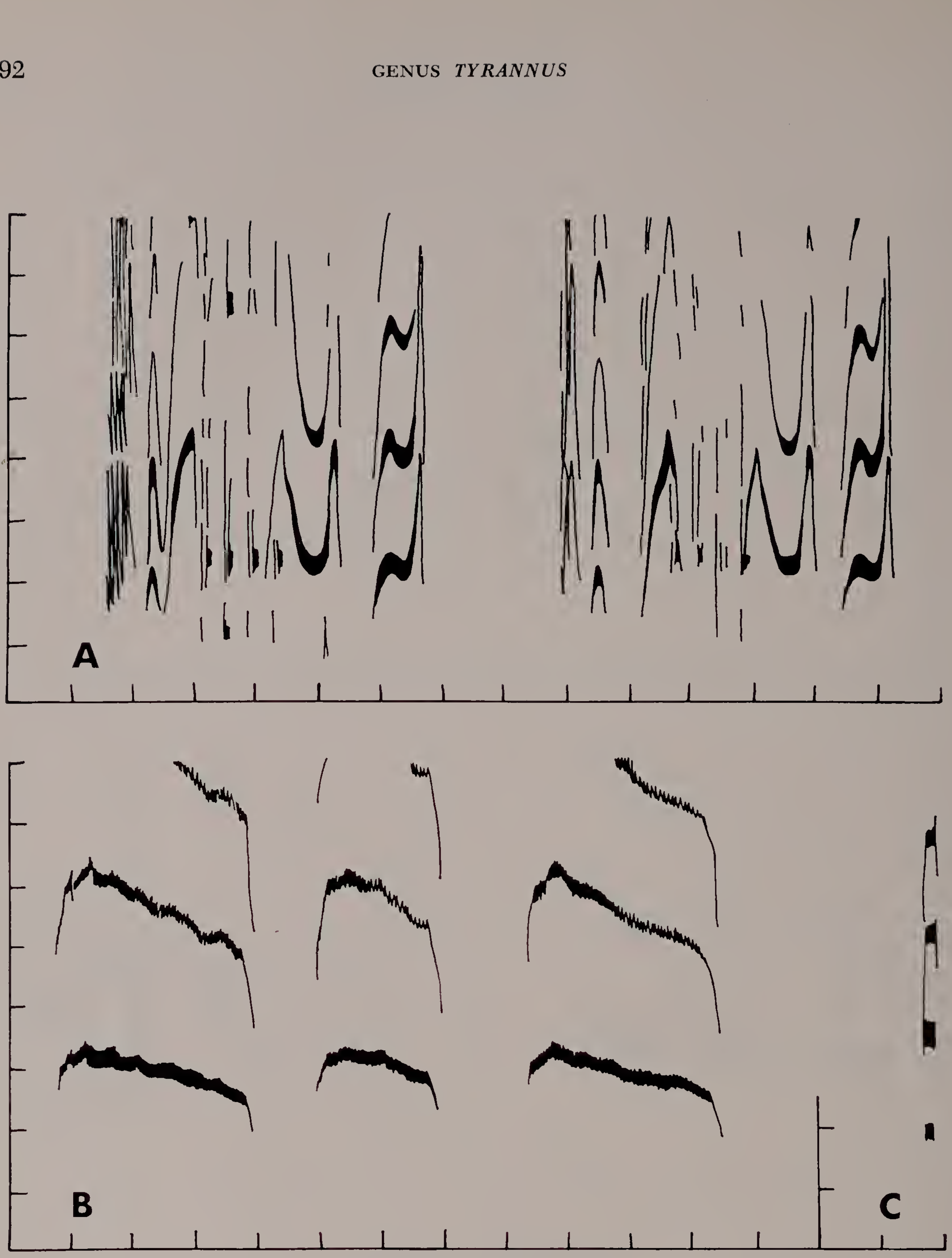
Tyrannus verticalis

FIGURE 4:3a. CdV, preceded by an ILHV, by an individual countercalling in post-RRV period.
4:3b. Part of a CV series (not from start).
4:3c. Start of a CV burst by a male greeting his mate at the nest.



Tyrannus verticalis

FIGURE 4:4. RRV, a complete example (0.2 seconds of silence deleted between the two lines).

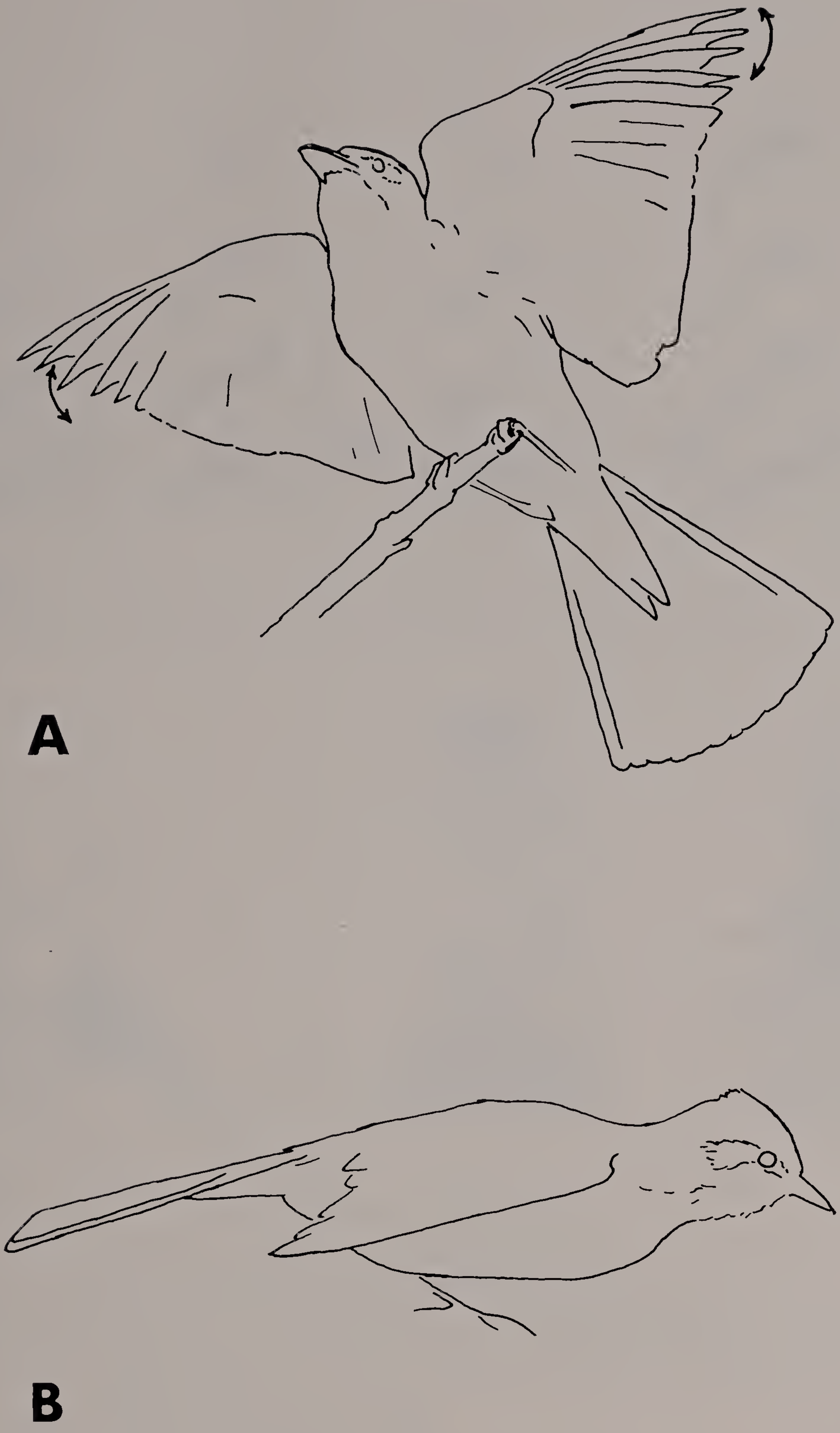


Tyrannus verticalis

FIGURE 4:5a. Two successive vocalizations and Wing Whirrs from a Tumble Flight display (timing preserved). Compare with RRV.

4:5b. Three successive examples of begging call of young on the day of fledging.

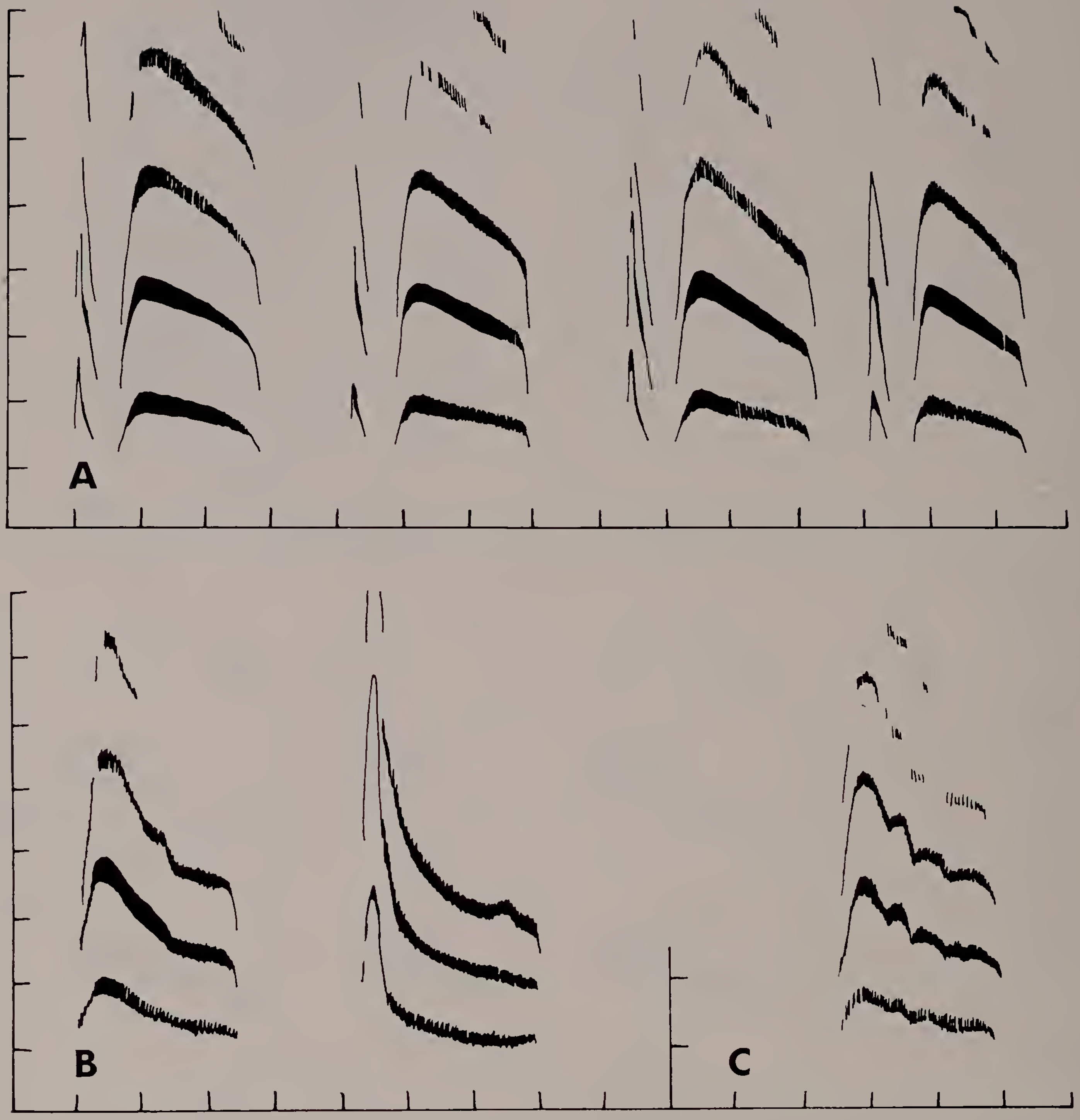
4:5c. Brief vocalization of nestlings.



Tyrannus verticalis

FIGURE 4:6a. Perched, guarding male (note emarginated outer primaries) greets mate with a WFt as she returns. He had just given a brief LHV, then shortly ceased WFt.

4:6b. Crouch of male in an encounter with an intruder.

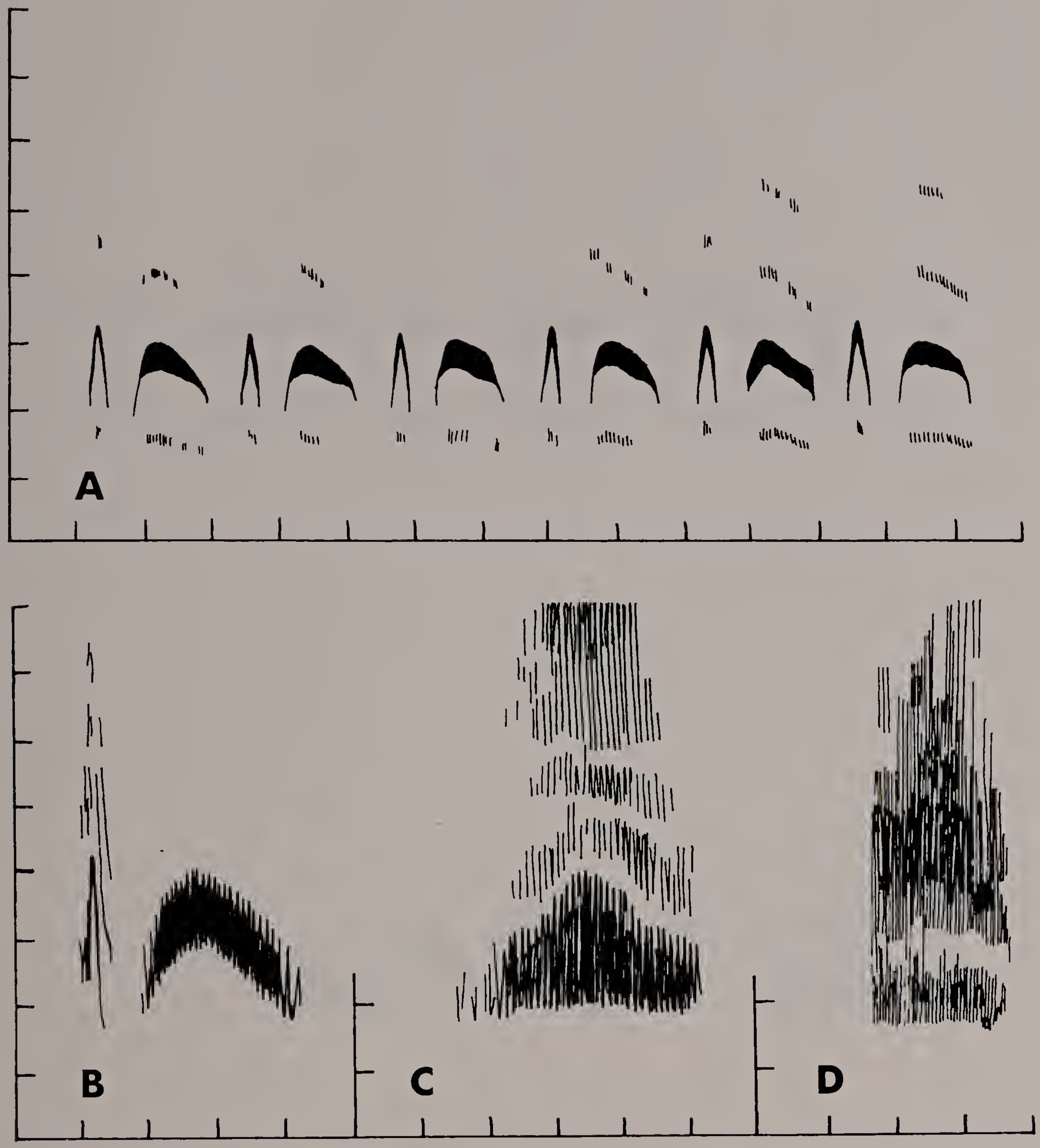


Tyrannus vociferans

FIGURE 4:7a. LHV of male greeting mate (her calls not shown).

4:7b. Two examples (not consecutive) of LHVs of females in greetings with their mates.

4:7c. A multipeaked form (not an extreme) of female LHV in a greeting.



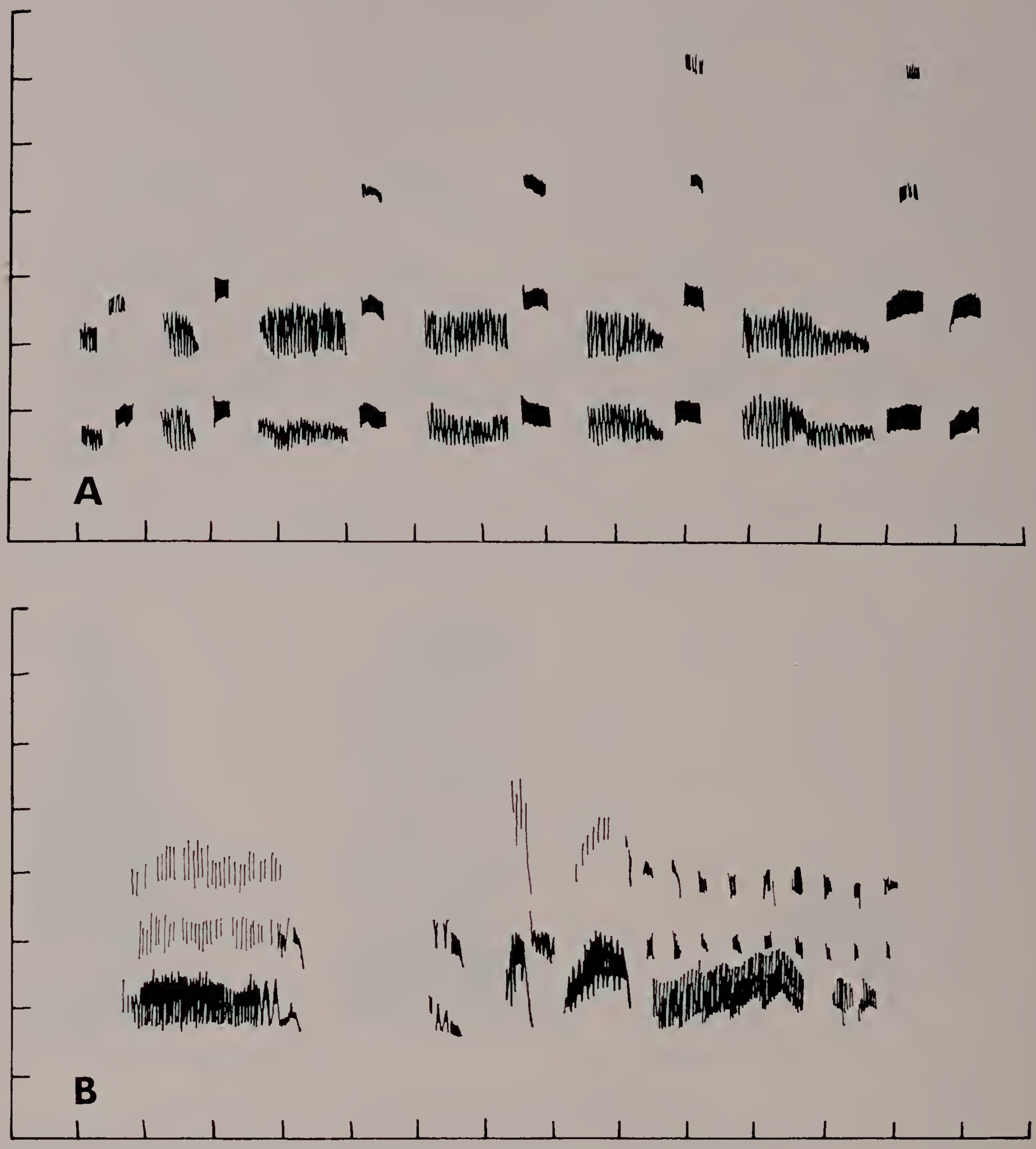
Tyrannus vociferans

FIGURE 4:8a. Portion of a CdV (not from start) countercalling with another male using same vocalization. Not all CdVs have units as brief as in this example.

4:8b. RHV, by a guarding male.

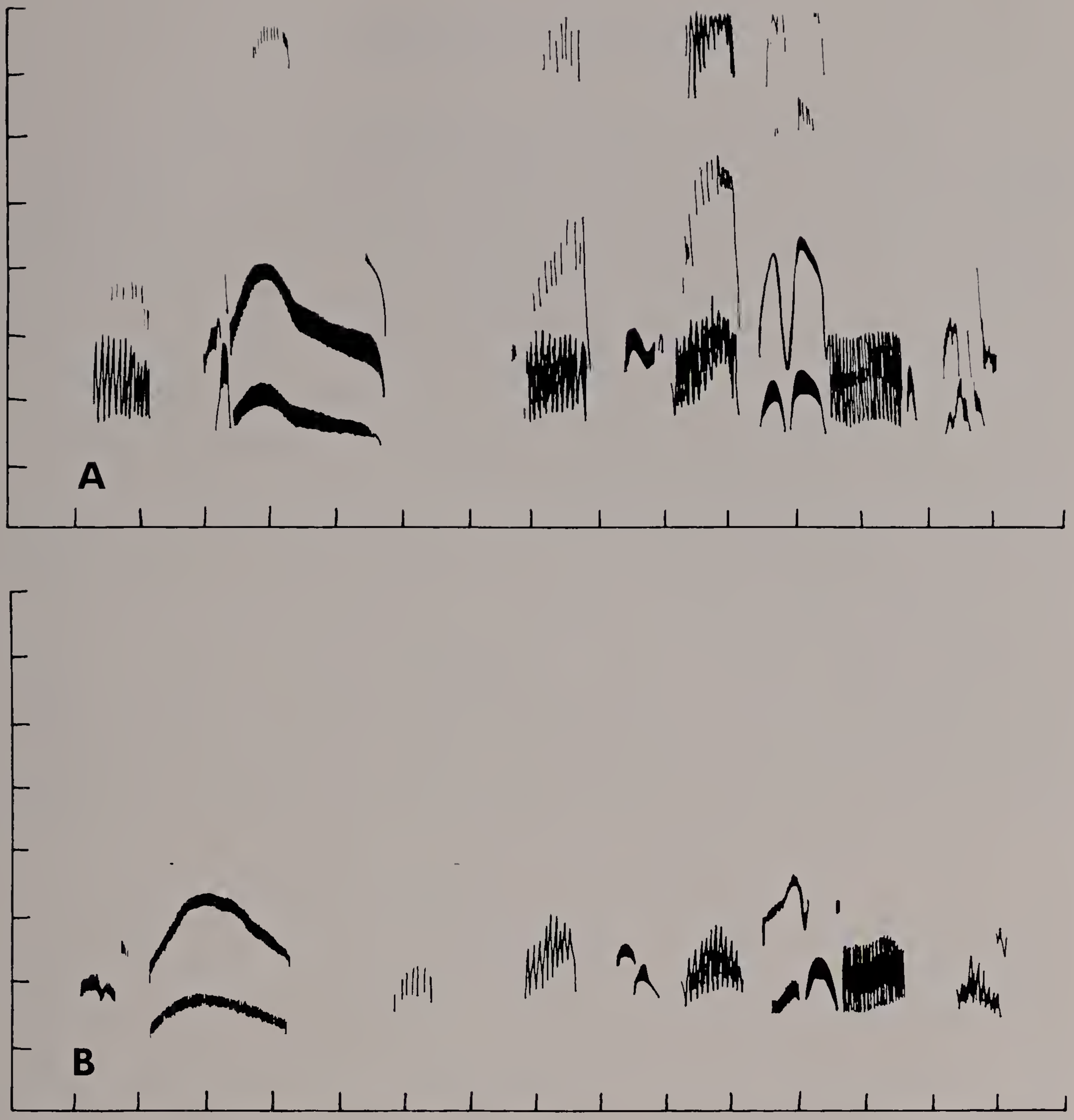
4:8c. SRHV, by a guarding male.

4:8d. One of several harsh calls from the start of a Tumble Flight.



Tyrannus vociferans

FIGURE 4:9a. CV, probably by a male.
4:9b. Variant of the RRV phrase used in Tumble Flight.



Tyrannus vociferans

FIGURE 4:10a. RRV, from predawn twilight.
4:10b. RRV, by a different individual in late evening twilight (some loss of fainter harmonics due to recording at a much greater distance).

Chapter 5.

MEXICAN SPECIES

Tyrannus crassirostris, Thick-billed Kingbird

The palest of the western and Mexican species, *T. crassirostris* has a back that is pale gray-brown. The head, wings, and tail are a darker gray-brown, but still fairly light; the darker brownish-black mask on the side of the face is not particularly conspicuous. The white throat grades into a slightly grayish chest and thence to a very pale yellow belly. The head and bill are both large, and there is a concealed yellow crown patch. The species breeds in the arid western portions of Mexico; its northernmost populations may move southward in the winter.

I observed this species in 1962 on 18, 19, and 20 June along the Rio Sonoita in southern Arizona at a site about 15 miles north of Nogales. Three males were located, one of which had a mate who was building a nest in the crotch of one of the uppermost limbs of a sycamore tree. In mid-afternoon on 19 June I watched a foraging bird, who did not display, along the Rio Magdalena about 8 miles below Imuris in Sonora, Mexico. Finally, late in the afternoon of 6 July I observed what was probably a patrolling male in Guadalupe Canyon of the Peloncillo Mountains of extreme southeastern Arizona. All of my observations were made at the northern extremity of the species' range.

Locomotory Hesitance Complex of Vocalizations

The LHV form used by males begins with a single, unpeaked, prolonged, harsh unit, succeeded by a series of 12 to 15 brief, harsh, downward slurred units, identical except at times for the ultimate one which may be at a lower frequency. The whole vocalization lasts just over a second (fig. 5:1a). In the field I occasionally noted that the one female I watched sometimes used similar or identical calls, but none of these was tape recorded, and I am inclined to be cautious about my ability to distinguish them with certainty after so brief an acquaintance with the species. The customary female form of the LHV at the Rio Sonoita site was a much shorter call than the male's. It also began with a single, usually prolonged harsh unit, although at a slightly lower frequency than the male's, and terminated with a relatively clear-sounding "tchee" (fig. 5:1b). Sometimes an additional brief "tch" was inserted between these two units; this was usual in the first of two LHVs when the female gave two in quick succession. The female might repeat her LHV once or even twice during a burst of LHV by her mate, but never seemed to pattern these repetitions into a series of more than two. She might also follow her first LHV with one or two slightly different calls which appeared to be contractions of it (fig. 5:1c) but these, too, did not appear to be grouped into a fixed pattern. The calls of both sexes were almost explosively loud.

The male LHV was used mostly in greetings (it was the only call he used in greetings in which the female also called) and once or twice as he was landing from a flight in what may have been patrolling. In form it is very like the CdV, and at least a few intermediates were recorded (see under CdV). The female always used her LHV in greetings with her mate. She also almost invariably uttered it as she flew from the nest she was building, but almost never on flying to the nest.

Sometimes after an LHV exchange with her mate the female would utter her CV as she settled into the nest, but this was likely only if he was perched close by. Once the male flew to the nest as the female flew in from a trip after collecting nest material. She was silent, and he did not call as loudly as he usually did in greetings, but his calls were most interesting. First he gave a short burst (nine units in just over one-half second) of CV which arched up in frequency, and the last six units had strong frequency fluctuation (i.e., were harsh). This was followed (fig. 5:2) by a five-second series of harsh units, which, in the last half also arched upward in frequency on two occasions; these upward archings are somewhat reminiscent of a call which was interspersed with the RRV calling (q.v.) of a different individual. The harsh units of the long series varied between about 0.1 and 0.2 seconds in length. At first each was made up of a brief loud element followed by a prolonged, slightly fainter element, and appeared very much like the reverse of some of the few CVs I have recorded from *T. vociferans.*

The higher harmonics of the prolonged portions could be resolved into two to many successive amplitude fluctuations, however, and in the main body of the five-second series these actually broke up into tenuously connected amplitude and frequency fluctuations (see again fig. 5:2). The net effect of these changes was to make each unit of the series appear in Sona-graphic analysis *very* much like the multi-peaked forms of the LHV of *T. vociferans.* Thus this once heard (and tape-recorded) vocalization of a male *T. crassirostris,* which would seem to be an intermediate between a CV and a LHV, showed strong resemblances to forms of both the CV and LHV of *T. vociferans.* Furthermore, it was extremely similar to most of the harsh calls used by male *T. verticalis* in fights and by males of that species when approaching their mates after being aggressively aroused.

A Brief Vocalization

Both sexes use a loud "tch-uhrreeE" of about 0.2 to 0.3 seconds in duration (fig. 5:1d). It seemed to ascend abruptly in pitch, and was rather rasping. The female I watched nest building almost invariably uttered this call from one to several times as she came back into the nest tree. Rarely she uttered her LHV instead, or uttered this call instead of an LHV on leaving the nest. Occasionally she stopped in the tree either before going to the nest or after coming from it, and usually called this "tch-uhrreeE" several times. Her mate used the same call infrequently while foraging on a nearby hillside, and the other male with which I worked in this region sometimes repeated it in his post-RRV calling. On 6 July in Guadalupe Canyon I watched a bird which was apparently patrolling after a rain squall. It moved from tree to tree using this call and others (described under CdV).

The available evidence does not permit this call to be assigned to any particular category; it could be ILHV, RV, or an RHV.

Attack and Attackee Vocalizations

The nest-building female was highly aggressive toward several birds passing close to her nest, and I twice recorded her as she chased away a male *T. verticalis* who often perched nearby. In one case she uttered a burst of seven harsh, very brief calls, probably a CV variant, and followed this with three "tch-uhrreeE" calls as she came back into the nest tree. In the other case she gave first a low-pitched harsh call which has three peaks and looks much like the male CV variant described above under LHV. As she continued to press the chase she gave a harsh "tchurr-t" (the first part of an LHV); after the chase she gave a single LHV with an abbreviated initial portion. On another occasion I saw but did not tape record a male *T. crassirostris* chasing a pair of *T. vociferans* from a tree. He uttered a harsh "ruhr" at the moment of actually striking at one of them and then two clearer "tch-rroy" calls as he chased them away. Probably in most of these cases the harsh calls at least were related to AtVs, even though none of them may have been an AtV; the clearer call may have been an AeV.

Chatter Vocalization

The nest-building female frequently called not only on her way to and from the nest, but also while in the nest, building. Most of the calls given from the nest itself were clearly CV (see fig. 5:3a). While she might go on calling for a prolonged period, most of the CV series were only about 20 to 30 units long. Most such series were marked by both an introductory unit and a terminal unit, and were usually arranged into couplets and some triplets, with occasional regions of several slightly harsh units. At least once she introduced a prolonged, wheezy "rheeez" (about 0.3 secs.) into a series. Another series of 18 units had triplets and couplets arranged in ascending frequency (within each triplet or couplet) and was followed by five spaced-out single units; this was after she had returned to the nest having chased a passing Phainopepla (*Phainopepla nitens*). The repeated arrangement of associated units in ascending frequency may have been only a stark representation of the overall, gentle, sinusoidal fluctuation in frequency which apparently characterized most of her other CVs. The loudest vocalizations occurred when she appeared to be agitated, and were remarkably loud for a CV given from the nest; this species, however, has remarkably loud calls for the most part.

A prolonged call thought to be a harsh CV/LHV intermediate was given once by a male and has been described under LHV.

Compound Vocalization

The CdV is a relatively prolonged vocalization, apparently used only by males. It is rather variable, and may begin with a "tch-uhrreeE," which leads into a long, rasping, descending tail (fig. 5:3b). The tail may be unbroken, may have one to several distinct brief sounds making up its terminal portion, or may start with similar brief sounds. The initial portion of the CdV may not be a "tch-uhrreeE," but one or two low-pitched brief sounds (fig. 5:3c) followed by one or two high ones (followed by the tail); sometimes a gap is left where the "uhreeE" portion might have been, sometimes not. But it is the tail that is the distinctive part of the CdV, and all of its variants are easily recognizable — even those in which the tail apparently fragments and becomes intermediate with an LHV.

This vocalization was given frequently by my one male who used the RRV, in the post-RRV period; all recorded samples of this had the "tch-uhreeE" at the start, and he was also repeating this call without the tail. Later, at 0715, on the morning of the 20th, I recorded him perched atop a tree and calling the CdV regularly, but mostly with only a couplet of brief introductory elements. The male, who guarded while his mate built, called a CdV at intervals, and these were highly variable in form. In Guadalupe Canyon, the bird apparently patrolling after a rain squall would stop in a tree, give a "tch-uhrreeE," then another with a few units appended, then gradually work into a CdV in which the tail was not noticeably fragmented. This could mean that the bird was adding a form of CV to an RV unit (if "tch-uhreeE" is an RV) and then gradually transforming this into a CdV — an interesting possibility when it is considered that the CdV appears to correspond in those species where it is known with the CV plus RV which make up the CdV of *T. tyrannus.*

Regularly Repeated Vocalization

The male whose mate was building apparently did not use the RRV on either 19 or 20 June, but another bird in the same region did, and I recorded him extensively on the 20th. The RRV began at 0415 with a few loud phrases apparently given in flight as the bird took up a station. There were fairly long pauses until 0435 after which calling was nearly continuous, but still noticeably irregular. The long pauses again became common, and it was over by 0500. He had changed perch only once during it.

There are two phrases to the RRV; "T t t t t, t T t tt rwheeuh t tt" (fig. 5:4a). These vary rather little in my sample, the first sometimes being a bit abbreviated and the second very slightly lengthened, and terminated in doubled units before the single unit; rarely, the two were run together. The pauses between the RRV units were longer than the pairs of phrases themselves most of the time, and in the interval just preceding a new pair of phrases the male often introduced a faint call. Sometimes these were simply extra first phrases, but usually they were different. A short one would have five units, the first unit like the start of a first phrase, the next three a descending set of very brief harsh units — apparently CV units — and the last like the terminal unit of a phrase two. Longer forms have up to eight units, and the most significant addition is a prolonged, downward-slurred penultimate unit (fig. 5:4b), which gives the call some semblance to a second phrase. In these longer forms the frequency of the resonance harmonics tends to rise, then fall; the similarity of the upward arced portions of some CVs has already been mentioned. I am quite puzzled by these calls, and regret that I have no further information about them.

Non-vocal Displays

Both sexes of *T. crassirostris* use a Wing Flutter display with the LHVs in greetings. A male I watched in late afternoon, who may have been patrolling while foraging, kept his Crown Ruffled. Other displays almost certainly exist, but were not seen by me.

TYRANNUS COUCHII, TAMAULIPAS OR THORN-SCRUB KINGBIRD

T. couchii is almost identical in plumage with *T. melancholicus,* and, as judged by its appearance, could be thought to be a large, slightly pale subspecies of that bird. Although originally described as a distinct species it has, in fact, usually been considered a subspecies of *melancholicus.* In its vocal repertoire, however, it is quite different from the Tropical Kingbird and quite clearly related to the other western North American and Mexican species. It ranges from southern Texas, along the lower Rio Grande (Rio Bravo del Norte) south through Tamaulipas to eastern Nuevo Leon, eastern San Luis Potosi, eastern Hidalgo, eastern Puebla, and northern and central Veracruz. At least the northern populations are migratory, and some birds are known to winter in southern Veracruz.

Since skins of *T. couchii* do not suggest that it is specifically distinct from *T. melancholicus,* and since current taxonomic works do not recognize it except as a subspecies of the latter, I was not originally aware that the northeast Mexican and Texas populations merited special study. In 1960 I obtained from the Cornell Library of Natural Sounds a recording of an RRV made near Valles, in the state of San Luis Potosi by L. I. Davis, identified as *T. melancholicus.* While I realized that this was different from any Tropical Kingbird I had heard in Panama, I had not yet done enough work with these birds to know what to make of the recording. In 1962, in Arizona, William Russell told me that he thought the local *T. vociferans* sounded rather like the kingbirds he had heard in the Rio Grande delta of Texas; when I argued that *T. melancholicus* did not sound at all like *T. vociferans* he called my attention to the description in R. T. Peterson's field guide (1961), which supported his contention. Later that summer he and I located a pair of *T. melancholicus* in northern Sonora, Mexico. These individuals sounded just like any other *T. melancholicus* I had heard, but they definitely did not sound to him like the kingbirds of the Rio Grande delta. Recalling Davis' recording of the RRV I decided that this population must be specifically distinct from *T. melancholicus,* especially as the family Tyrannidae is notorious for having many species of closely similar appearance but quite distinct vocalizations.

In 1964 my wife and I studied *T. couchii* from 15 to 24 May in Texas at the National Wildlife Refuges of Santa Ana and Laguna Atascosa in the lower Rio Grande valley. Later that same year we made a few observations (but did not make tape recordings) while on vacation at sites in northern Tamaulipas south to Antiguo Morelos, Tamaulipas, Mexico, on 2 and 3 August; on 9 and 10 August we observed what should have been individuals of *T. melancholicus* farther south (within 30 miles of the city of Veracruz, Mexico), and on 14 and 17 August we visited Bentsen Rio Grande Valley State Park in Texas to see the northernmost birds at the same stage of the breeding cycle as the Mexican individuals. The August observations are discussed separately from the description of the displays, below.

Locomotory Hesitance Complex of Vocalizations

The vocalization used by *T. couchii* males during greetings with their mates comprises a series of about three to seven asymmetrical harsh units. Often this LHV series is preceded by a single unit of much greater frequency spread, a harsh "tzheer" or "tzheeeeer" (fig. 5:5a), and in these cases the similarity with the male form of LHV in *T. crassirostris* is striking. Occasionally, the first unit of a series may begin as a "tzheer" and change to the form of the subsequent units. In highly active agonistic situations, as when a male encounters an intruding conspecific in the presence of his own mate and engages in fighting and chasing, much of his vocalizing during exchanges with his mate comprises LHVs, but the serried units attain two to four (often three, fig. 5:5b and c) peaks as in *T. vociferans.* Males almost always use the WFt display with this vocalization. Both vocalization and WFt seem to be restricted to greetings, though, and I have not known them to be used at other times when a state of locomotory hesitance might be expected. This is perhaps in part a result of my brief experience with the species, as I failed to see certain kinds of situations (for instance, I saw nothing I could be sure was patrolling).

The vocalization used by females during greetings seems to be much more varied than the male form, but also shows close similarity with the form of the female LHV of *T. crassirostris.* The most striking, and sometimes the only, part of the vocalization is a high-peaked, asymmetrical unit very much of the form of its counterpart in *T. vociferans* (fig. 5:6a). This portion varies within rather narrow limits, but is usually prefixed by a harsh sounding portion which is extremely variable (fig. 5:6b to i shows most of the forms known) and which at times, like the male form, follows or even incorporates a "tzheer" unit. Incorporation of the "tzheer" (fig. 5:6 h and i) as a prefix seems fairly rare, and usually occurs when a female is interacting with a highly agitated mate. In greetings with her mate a female usually uses about one to four units at irregular intervals during his call; she may, however, use up to three or more sets of couplets (fig. 5:6c, very reminiscent of *T. verticalis*) or from four to ten simple units (fig. 5:6b) in a series, evenly spaced or gradually slowing. The vocalization is accompanied by a WFt.

T. couchii females also use their LHV in at least one situation which is not a greeting. Two of the individuals we watched (one was beginning to incubate, and the other, more vociferous, was nest-building) usually called on leaving the nest if we were standing and watching within 50 yards. They would not fly directly away, but would go first to a favored perch within a few feet of the nest. On landing on this perch a brief LHV with WFt was customary. Many of these calls were recorded from the building female, and most were of forms d through i of fig. 5:6, even on the relatively few occasions when her mate was present.

Repeated Hesitance Vocalization

While the vocalization "tzheeeer" is often an integral unit in both of the LHVs described, it also occurs alone and is probably comparable to the RHV and SRHV of *T. vociferans,* being used in situations where ILHV or RV would be used by *T. tyrannus.* Birds of either sex sometimes use a brief form (fig. 5:7a) in flight, usually shortly before landing. A more prolonged form (fig. 5:7c) may be given on or just after landing, and use of either form is in most cases without a WFt display. At least some individuals repeat this form when going to roost in the evening. In prolonged agonistic situations resulting from frequent intrusions by one (perhaps usually the same) conspecific into the immediate vicinity of the nest of one pair, the pair members often exchanged "tzheeer" calls while perched, and used LHVs only if one of them actually flew. In these instances some WFts were used with the RHVs; the female usually gave the brief form typical of flight or landing, and the male a slightly or considerably longer form. More prolonged variations occur in different situations and are discussed under CdV and CV.

Compound Vocalization

One sort of prolonged "tzheeeeerrhhh" call (fig. 5:7b and d) may for comparative purposes be named the CdV, although there is little to suggest that it is actually compounded of elements or units of other displays. (Rarely, though, it does fragment into a brief CV terminally, suggesting that it *might* be compounded of an RHV + CV units.) It is one of the most noticeable calls of the species, and reminded us of the "tzeer" RV of *T. tyrannus,* with which it probably shares most aspects of message. The longest forms are probably used solely by males, although at times I think females use calls longer than the usual RHV, which might be brief CdVs.

The CdV is usually given by a perched male that appears to be guarding. It is sometimes given in flight and even on landing (without WFt) by birds which are either guarding or patrolling (at times there may be no meaningful distinction between the two activities). After a bout of defense activity, such as chasing a Mockingbird from near the nest, a male is likely to take up a guard perch and call the CdV frequently. During prolonged and fairly rapid repetition of this call, frequently an occasional (and sometimes imperfect) RRV complex phrase may also be uttered. The CdV is virtually the only call used in daytime countercalling. For probable usage by a female see under ILHV.

Incipient Locomotory Hesitance Vocalization

The ILHV is a simple, chevron-shaped vocalization with some variation in pitch (fig. 5:8a). It is sometimes used by guarding males, particularly if they are agonistically excited and flying about near or in the nest tree; it is, however, much less typical of guarding than is the CdV. When both of the vocalizations are being used, some of the CdVs may follow as closely as 0.1 second after the last preceding ILHV, and this happens often enough to suggest that the combination may itself be almost formalized.

T. couchii females, on the other hand, often utter the ILHV on approaching the nest if they are made nervous by the presence of observers. The nest-building female was particularly regular about this. Each time we arrived on our observing stations she would hesitate on coming to the nest, stop on a number of perches including her usual perch about five feet from the nest, and utter the ILHV frequently. Eventually she would enter the nest and work on it, continuing to utter the ILHV (note, not the CV in most cases). On leaving she would stand up in the nest, utter an RHV, fly to her perch five feet away and land with a brief LHV and WFt, remain there for a few seconds to a minute, giving occasional calls which were either long RHVs or CdVs, and finally fly off and collect more material. In each session of observation she would gradually become less disturbed, and approach the nest more directly and finally silently, but would usually continue using the ILHV from the nest while working, and would utter her other vocalizations on leaving the nest and when on her perch. We were never able to detect any patterned series in her ILHV calling, or in that of any other individuals we studied in Texas.

ILHVs were also used by both pair members along with RHVs and forms of the LHVs when a migrating Swainson's Hawk (*Buteo swainsoni*) flew close past a nest and was mobbed. During encounters between pairs and intruding conspecifics the ILHV was used commonly, apparently by all kingbirds. In one recorded face-to-face fight of two kingbirds there were brief RHVs (the typical flight variation), modified harsh units from LHVs, and many ILHVs. Of the latter, one set of seven is highly varied, the ILHV units being extended and forced into a succession of minor peaks (fig. 5:8b), perhaps a modification of the sort seen in the LHV units, or perhaps in the direction of intermediacy with the CV.

Likely the message of the ILHV in *T. couchii* does not fully correspond to the message of the ILHV in *T. tyrannus,* but includes some aspects of that message and some aspects of the CV message of the latter species. The CV of *T. couchii* seems to be more restricted, and usually to have an aggressive overtone.

Chatter Vocalization

The CV of *T. couchii* comprises series of units comparable with the relatively elongate units of the other western and Mexican species, rather than with the simple, brief chevrons of *T. tyrannus.* Most units are about 0.1 second in length, but some may be slightly shorter or more than twice as prolonged. They may be nearly flat or slightly humped with little frequency fluctuation, or have as drastic frequency fluctuation as has a "tzheeer" call; various forms are illustrated in fig. 5:8c and 5:9a, b.

Females utter the CV while nest building or while settling to incubate if they appear to be at least slightly nervous. This use was rare, however, in the absence of a guarding mate. The individual we watched nest building almost always called in the nest while working, and gave every indication of being slightly anxious about our presence. Her mate was rarely present on a guard perch, however, and on only one occasion did we record a CV from her in his absence; in that instance the call was brief (about 2.5 second) and harsh and was soon succeeded by ILHVs. Her usual call, as has been mentioned, was the ILHV, and she repeated it frequently although never in a patterned series. Likely neither CV nor ILHV is fully homologous with the call of the same name in *T. tyrannus* (see Chapter 9).

Occasionally a female switches from an LHV exchange with her guarding mate to a CV as she enters the nest. In some cases, she may begin the CV directly as a suffix to her LHV.

Males of *T. couchii* probably have a nest-site-showing display, since the male whose mate began incubation during our observations was seen on several occasions entering the nest. Once he did this in her absence, uttering a brief CV during the first of the five seconds he spent in the nest. Another time the pair had a prolonged interaction when the male entered the nest as his mate landed within a foot of it and both repeated CV series over and over. On no occasion was the action followed by any other activity than the male leaving the nest and the female, if she was present, entering it; if the male's actions are a formal display they are probably relevant earlier in the cycle, and they almost certainly do not function as a precopulatory display. Both individuals prefixed most of their CV series in these cases with modified RHV or CdV calls in which the frequency flattened out at a rather high level (fig. 5:9a) and maintained this until the end of the vocalization where it dipped slightly. Ensuing CV units closely resembled the terminal portion. Where this unit was not used, most CV units were harsher, and resemble the terminal part of any of the various "tzheeeeer" calls.

Regularly Repeated Vocalization

The RRV of *T. couchii* is not really arranged in phrases, but rather has a variable and hesitant-sounding prologue which leads to a relatively invariable and complex phrase (fig. 5:10). In the prologue there is a number of modified "tzheeeer" calls, then sometimes some irregular couplets of what appear to be prolonged ILHVs. In some individuals the elements of the couplets are joined, and the form of the modified "tzheeer" calls also seems to be different in different individuals. The complex phrases are also individually specific, but the differences between them are less marked; nonetheless, each of the individuals we recorded is consistently recognizable by his complex phrase. While the repetitions of "tzheeer" in the prologue are reminiscent of *T. vociferans,* the complex phrase is quite similar to that of *T. verticalis.* Except for generic similarities that characterize most of the RRVs of the various kingbirds, there is no obvious reason to ally

T. couchii with *T. melancholicus,* the species of which it has been considered a subspecies.

In the dense population of *T. couchii* at Santa Ana most or all males called the RRV almost continuously throughout the predawn twilight. Each male usually called from one or a very few perches. Countercalling sometimes continued until an hour or two after sunrise, even on sunny mornings, but it was always more irregular than the continuous RRV calling. Usually the prologue portions of the call became relatively more common than the complex phrase, and occasional modified ILHV couplets or even single, unmodified RVs occurred among the modified "tzheeer" calls. Some of the "tzheeer" calls were also unmodified, and appeared to be RHVs, but the more prolonged CdVs were rare or absent in the post-RRV calling. During a particularly prolonged and occasionally violent dispute between a guarding male and a conspecific (sex not known) which persisted in approaching the nest, at least the defending bird used some phrases, and these were variously foreshortened and had most or all of the elements made confluent.

Vocalizations of Fledglings

On 3 August, 1964, and 17 August, 1964, fledglings were seen in the company of adults at Antiguo Morelos, state of Tamaulipas, Mexico, and at Bentsen Rio Grande Valley State Park in Texas, respectively. In all cases the fledglings begged from the adults, using faint, wheezy calls, transcribed in the field as "wheeee" or "weeee"; these vocalizations were reminiscent of the calls of begging fledglings of *T. verticalis,* but I have no recorded samples for analysis. As in the case of young of other kingbird species, there was no wing fluttering during begging.

Non-vocal Displays

Unfortunately, no Tumble Flight was observed, although the high population density and frequent agonistic encounters with intruders would seem to be ideal situations for eliciting such a display.

Use of a Wing Flutter with the LHV in greetings has already been mentioned. *T. couchii* usually leans slightly forward and holds its wings slightly above the back when fluttering; it also fans its tail, and quivers it (or quivered it in instances when I was able to obtain a good view through binoculars — this motion is slight and difficult to observe). In many of the instances where a pair and an intruding conspecific were all present in the immediate vicinity of one nest, and agonistic encounters were frequent, we saw cases of intermediates between the usual greeting display and the Crouch display. The defending male was particularly likely to begin an LHV with WFt and then lean farther forward and go into a full Crouch display with his wing tips drooping, wrists exposed, neck extended, and body held horizontal. His WFt would then change to a Wing Flicking display, and he would often attack the intruder using Bill Snaps, sometimes preceded by a Wing Whirr. At other times, the Crouch and attendant displays were not preceded by WFt. One morning he took a guard perch after having attacked and driven off a Mockingbird from near the nest, and began to utter CdVs at intervals of from three to 20 seconds. Frequently for about two minutes he would lean forward but not fully Crouch, fan his tail open and shut, and give little jerky flutters of the wings which were intermediate between WFt and WFk; these displays were not correlated with his vocalizations.

Crown Ruffled was also seen during most encounters, agonistic or otherwise, and was invariable with the Crouch. We did not see a case of Revealed Crown Patch, or of Raised RCP, but since a concealed patch exists in the center of the crown, it is likely that these displays do occur.

August Observations

In the late evening twilight of 2 August we heard "tzheeer" calls from several individuals which must have been going to roost at sites in second growth, thorny, forest within three miles of Antiguo Morelos. In the predawn twilight of the following morning (0540 to 0555) at least five individuals could be heard in one region just east of the town; all were repeating "tzheeeer," and two of them were occasionally uttering the complex RRV phrase. That the calling was more like post-RRV than RRV proper could easily have been due to the lateness of the season — local birds were seen with full-grown fledglings. The RRV phrases sounded just like those of the Texas individuals, and this is in agreement with the RRV recorded by L. I. Davis about 10 miles north of Valles (about 25 miles south of Antiguo Morelos); his recording is no more different from the RRVs recorded by us in Texas than the amount of difference we found between neighboring individuals.

In addition to the "tzheeeeer" calls, we heard a great many ILHVs, and once I heard what seemed to be a patterned series of ILHV which resembled the general form of a *T. melancholicus* prolonged LHV.

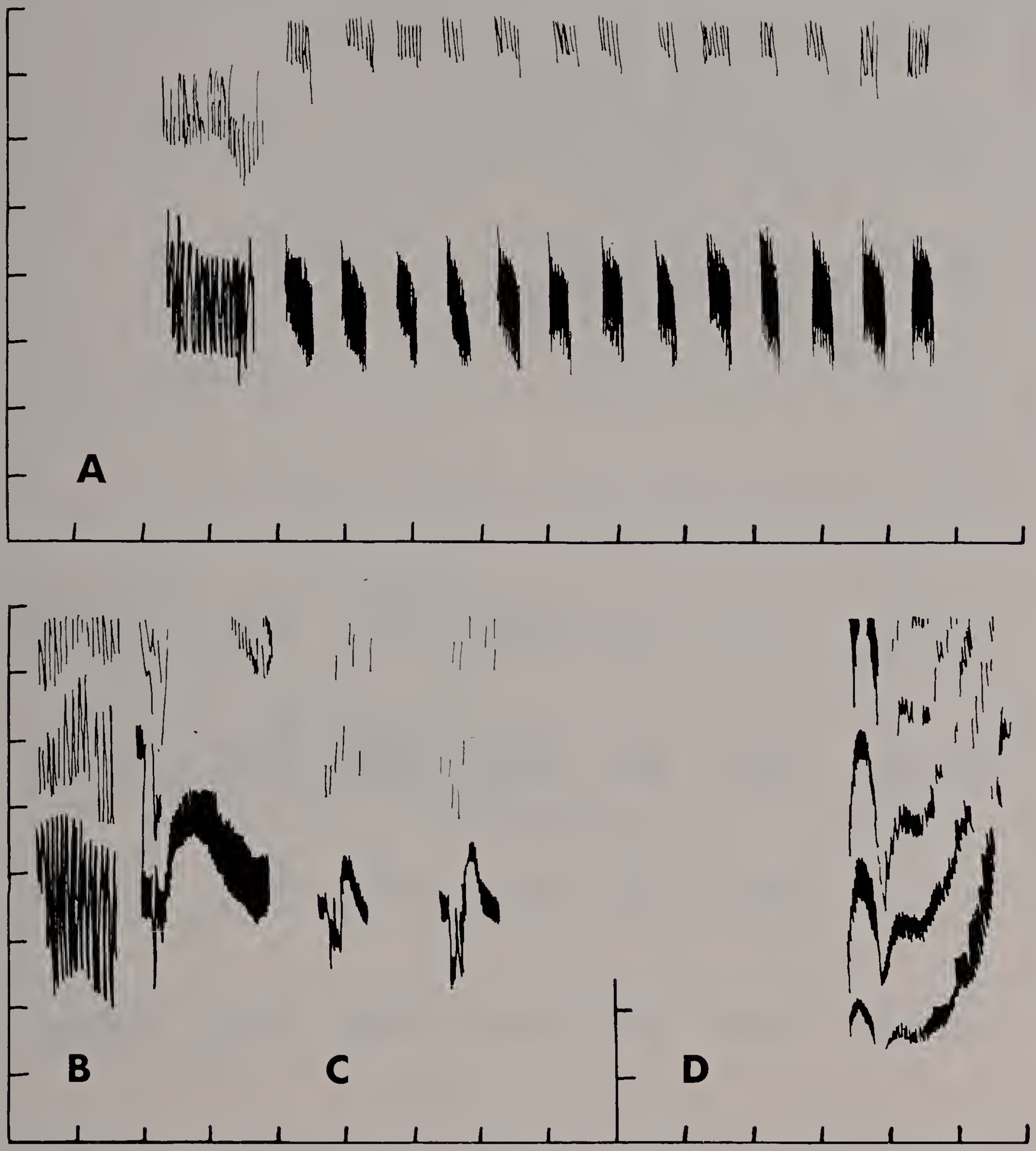
Late in the afternoon of 9 August, about 30 miles southwest of the City of Veracruz, we found at least two kingbirds in an area of pastured thorn scrub. These should have been *T. melancholicus* at about the northern limit of its range in that area. In fact, the site may be almost exactly the point at which L. I. Davis recorded the typical *T. melancholicus* RRV which is now Cut Two of that species in the Cornell collection. Several times, however, we heard them use "tzheeer" calls, and saw one greeting with WFt in which the calls used were *T. couchii* LHV. We lost sight of these birds and then found two within 50 yards, but do not know if these were the same individuals. One of these second two individuals was uttering occasional short bursts of what seemed to be ILHVs, and the bursts were patterned. Then the other individual flew toward it and one of them uttered a patterned series of similar units, apparently as a greeting. All of these calls were of the pitch of *T. couchii* but seemed to be patterned like the higher pitched LHV calls of *T. melancholicus.* The rate of succession of units within each patterned utterance was less than that typical of most *T. melancholicus* I have heard in various parts of the range of that species, but both the pitch and the rate strongly reminded me of the sound of a tape recording of its calls played at half speed. We lost these birds in the scrub, heard two more of the *melancholicus*-like "greetings," and then were forced by a heavy thunderstorm and oncoming evening to leave the area. The following afternoon in better weather we adjusted our itinerary to permit us to spend some time searching for kingbirds in the coastal plain up to 30 miles north of the city of Veracruz and we heard some of the shorter, "half-speed" *melancholicus*-type bursts of calls from another individual, but when we found the bird it remained silent as long as we kept it in sight.

Exigencies of time prevented further attempts to observe members of this population, but when we returned to Texas we altered our route and visited Bentsen State Park. Here the *T. couchii* were also in family groups of two adults and a set of fledglings, as they had been at Antiguo Morelos. The most commonly heard calls were an RHV "tzheeeeer" and simple wheezy begging calls by the young. In the evening a few individuals called a number of CdVs in slow succession, and others uttered occasional, scattered ILHVs with interspersed ILHV "tzheeeer" calls or simple "tzheeeer" calls. *No* patterned ILHV series were heard. When a Peregrine Falcon (*Falco peregrinus*) made a pass at a Willet (*Catoptrophorus semipalmatus*) on a mudflat, all members of the two families of *T. couchii* in the trees in the immediate area began to use RHV- and CdV-length "tzheeeer" calls, and some of them kept calling for nearly ten minutes. No ILHVs were used.

In sum, it seems that kingbirds in Veracruz and perhaps as far north as at least Antiguo Morelos use both *T. couchii* vocalizations and some other calls comprising units like the ILHV of *couchii* arranged in *melancholicus*-like LHV patterns. It is not certain that a single individual may use both sorts. The observations were made at a time when either adults were accompanied by fledglings or when birds appeared to be molting; these are unfavorable times to study vocal communication among unmarked and unknown birds. Yet these observations in part obscure the picture we had obtained of the vocal repertoire of *T. couchii* in Texas in the early stages of the breeding cycle. That repertoire was clearly distinct from the repertoire of *T. melancholicus* in so many characteristics that it is very difficult to doubt that at least the Texas kingbird population had a recent evolutionary history quite distinct from that of all known populations of

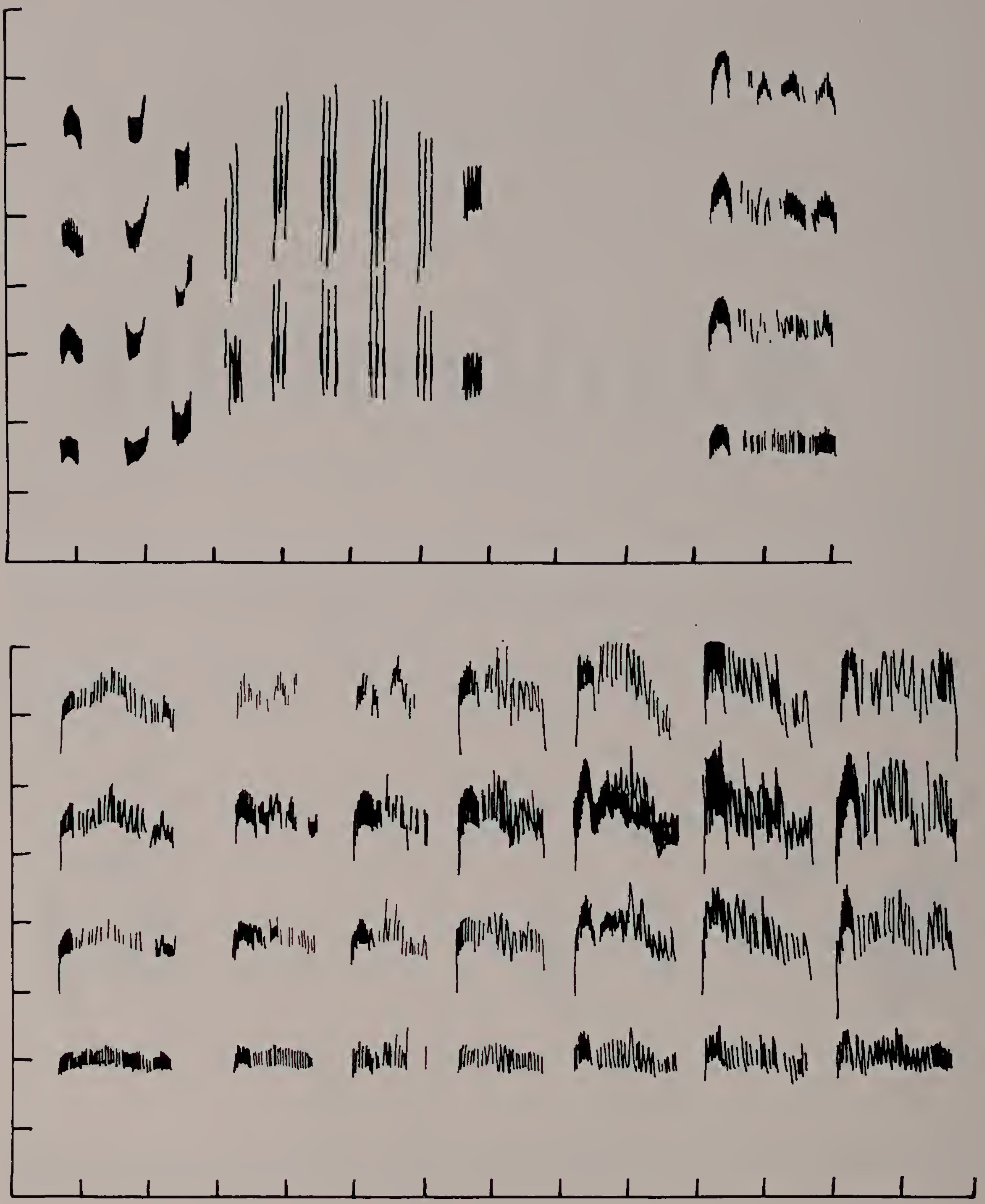
T. melancholicus. The similarities with *melancholicus* vocalizations may be peculiar to fledglings not yet proficient in their control of vocalizing, but there is little reason at present to suspect this should happen. A better guess, but still a guess, might be that such calls are peculiar to individuals in regions of low population density, and that the birds in the denser populations of the Rio Grande valley and Antiguo Morelos were less likely to use the ILHV in any form. Possibly there is a gradual dialect change in the repertoire of *T. couchii* as one moves southward — but why should such a change appear to converge with a *T. melancholicus* feature as the range of that species is approached? The birds in the vicinity of Veracruz should in fact, have been *T. melancholicus*, as judged by the subspecies assignations of kingbirds that have been collected there (*T. m. chloronotus,* see Lowery and Dalquest, 1951, and Warner and Mengel, 1951). Do the two species meet and hybridize? Has there been a recent breakdown of some extrinsic isolating barrier and subsequent genetic introgression? Do some individuals actually use at least parts of the repertoires of two different species, or some populations contain individuals which use one or the other repertoire? The last suggestions at least seem quite improbable, if only because they would interfere severely with communication. But the explanation of our few observations from these populations promises to be interesting, even if it must await further collection of data.

FIGURES



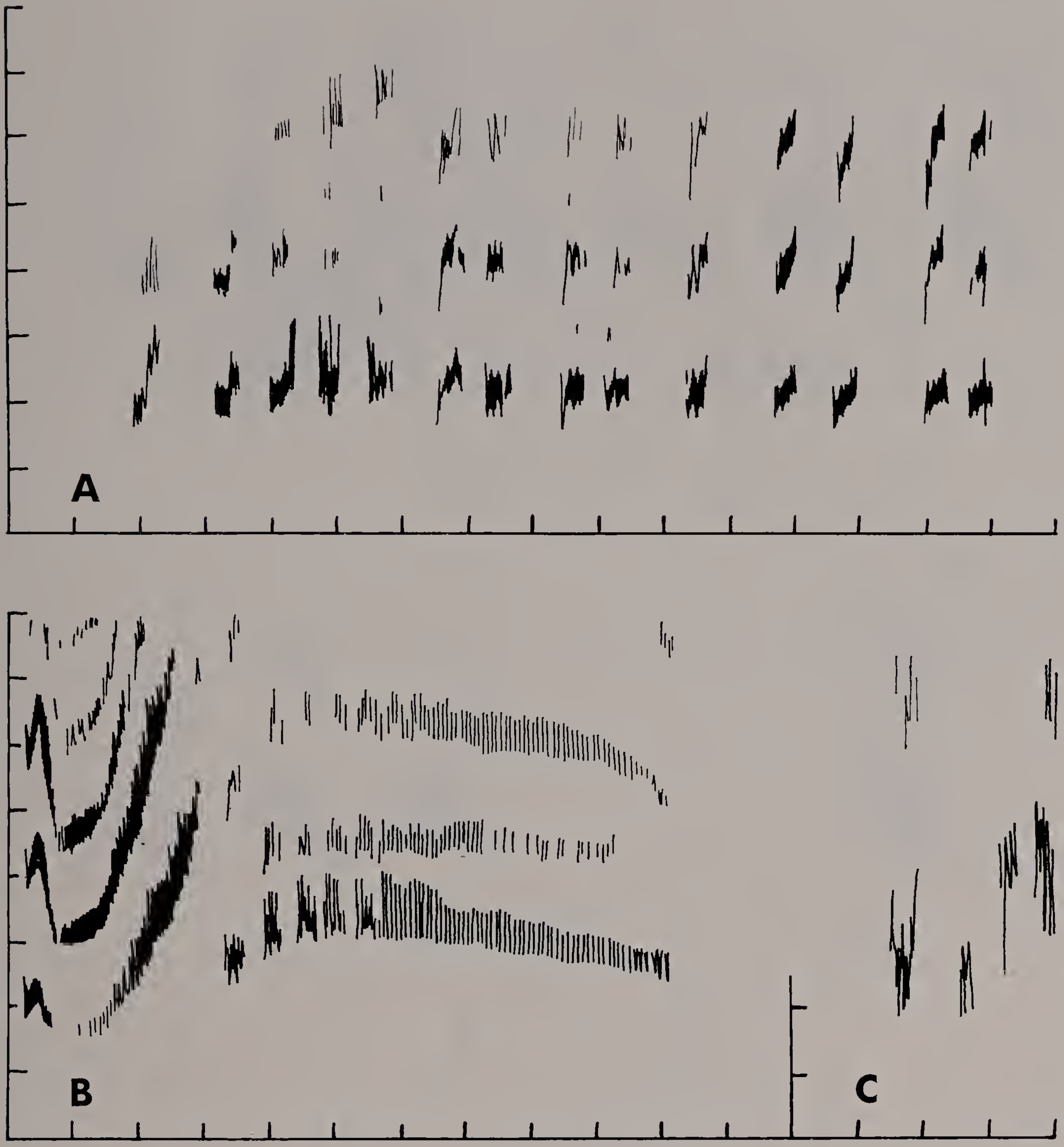
Tyrannus crassirostris

FIGURE 5:1a. LHV of male, greeting mate.
5:1b. LHV of female, greeting mate (whose call overlapped and is not shown).
5:1c. The two elements which may be added to the shorter female LHV; a longer female LHV comprises (b) plus (c) in the relationship shown.
5:1d. A loud "tch-uhrreeE."



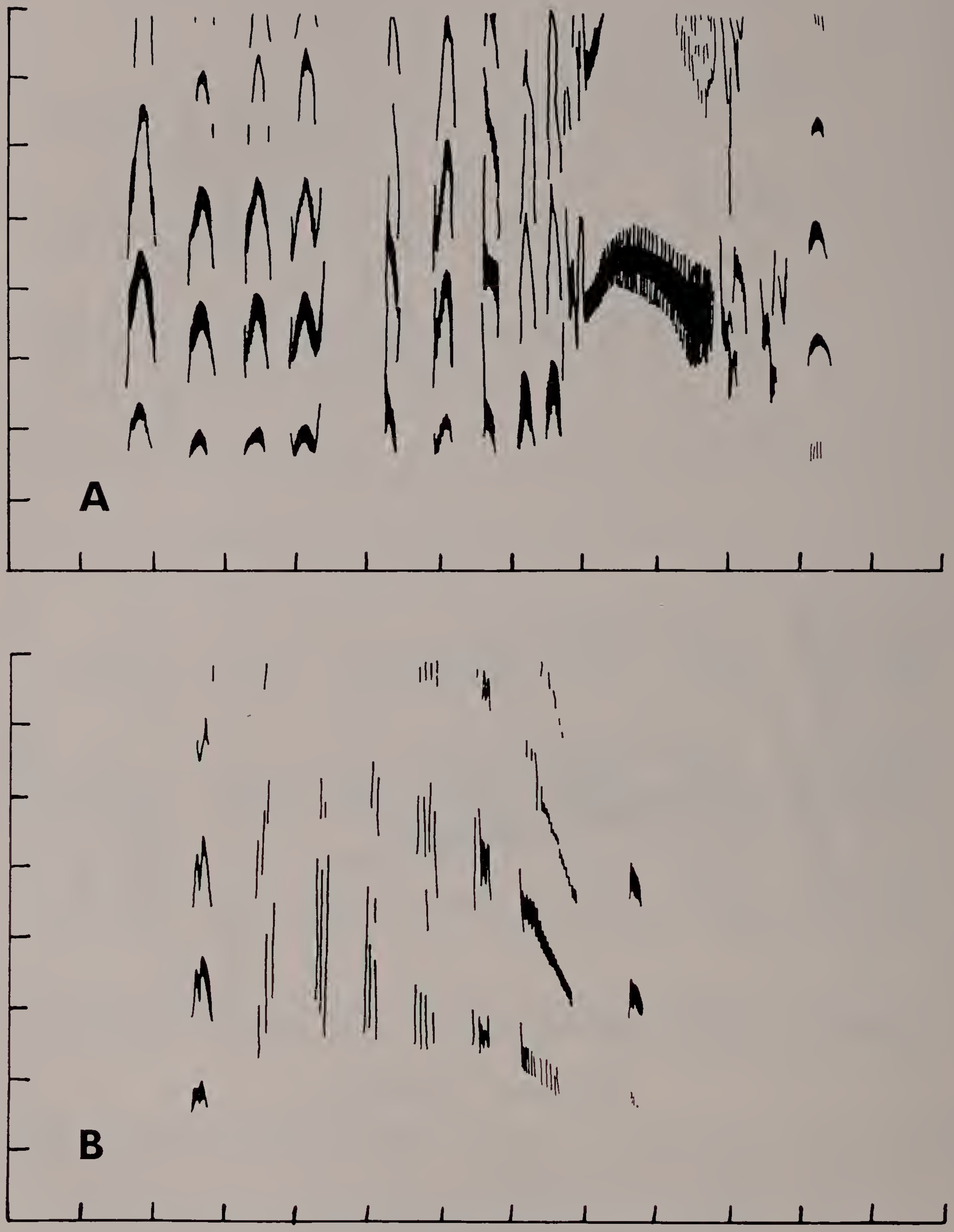
Tyrannus crassirostris

FIGURE 5:2. The apparent CV/LHV uttered once by the male flying toward his mate as she approached the nest. The initial short burst and the first unit of the much longer series are shown on the top line, the second through eighth units of that series below. (The separation between the lines is artificial; the long series was unbroken.)



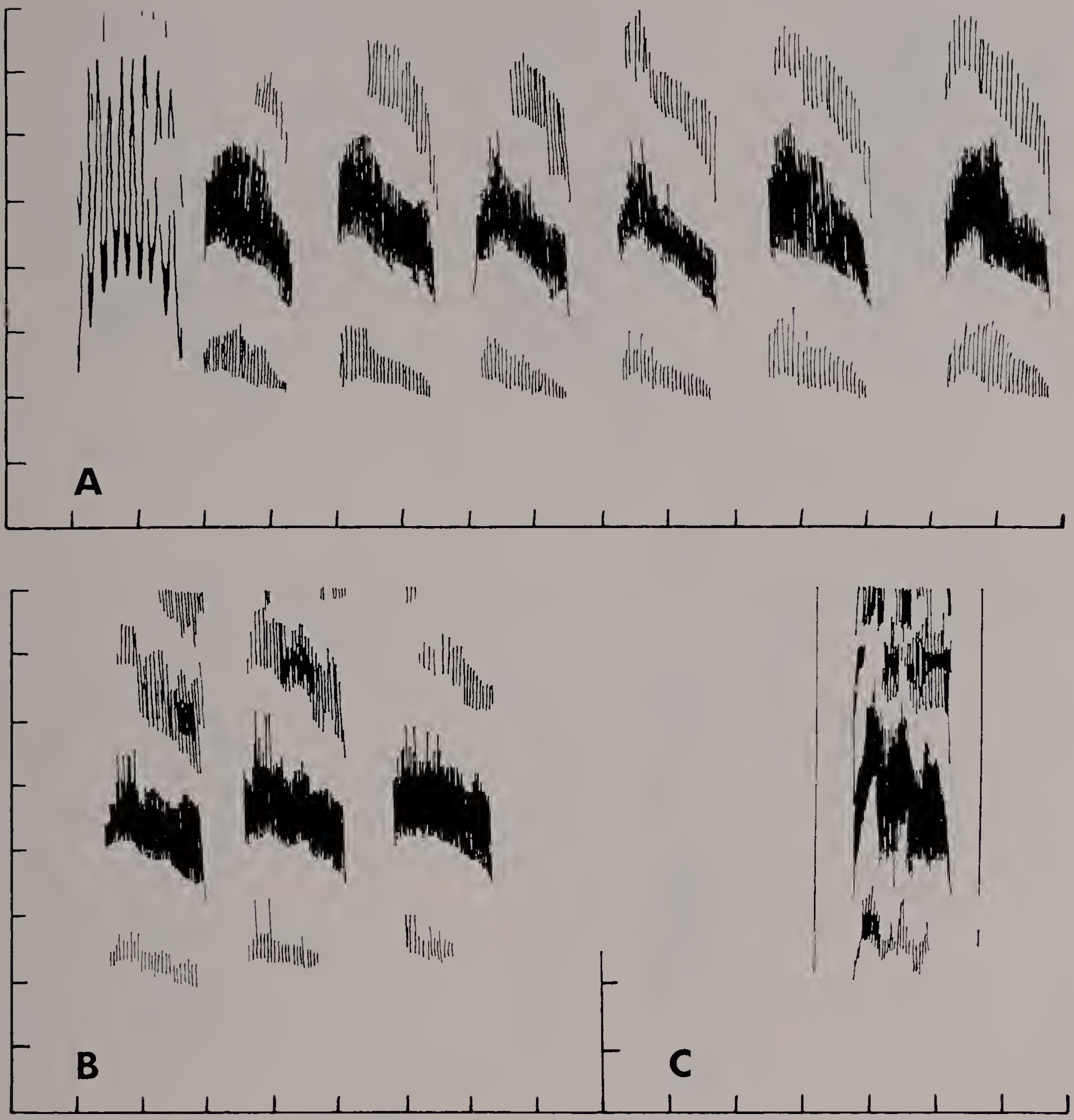
Tyrannus crassirostris

FIGURE 5:3a. CV—the first 14 units of a 23 unit burst by the female settling on her nest.
5:3b. CdV, by a guarding male.
5:3c. Alternative introductory portion of a CdV—this was followed by a prolonged harsh portion as in (b).



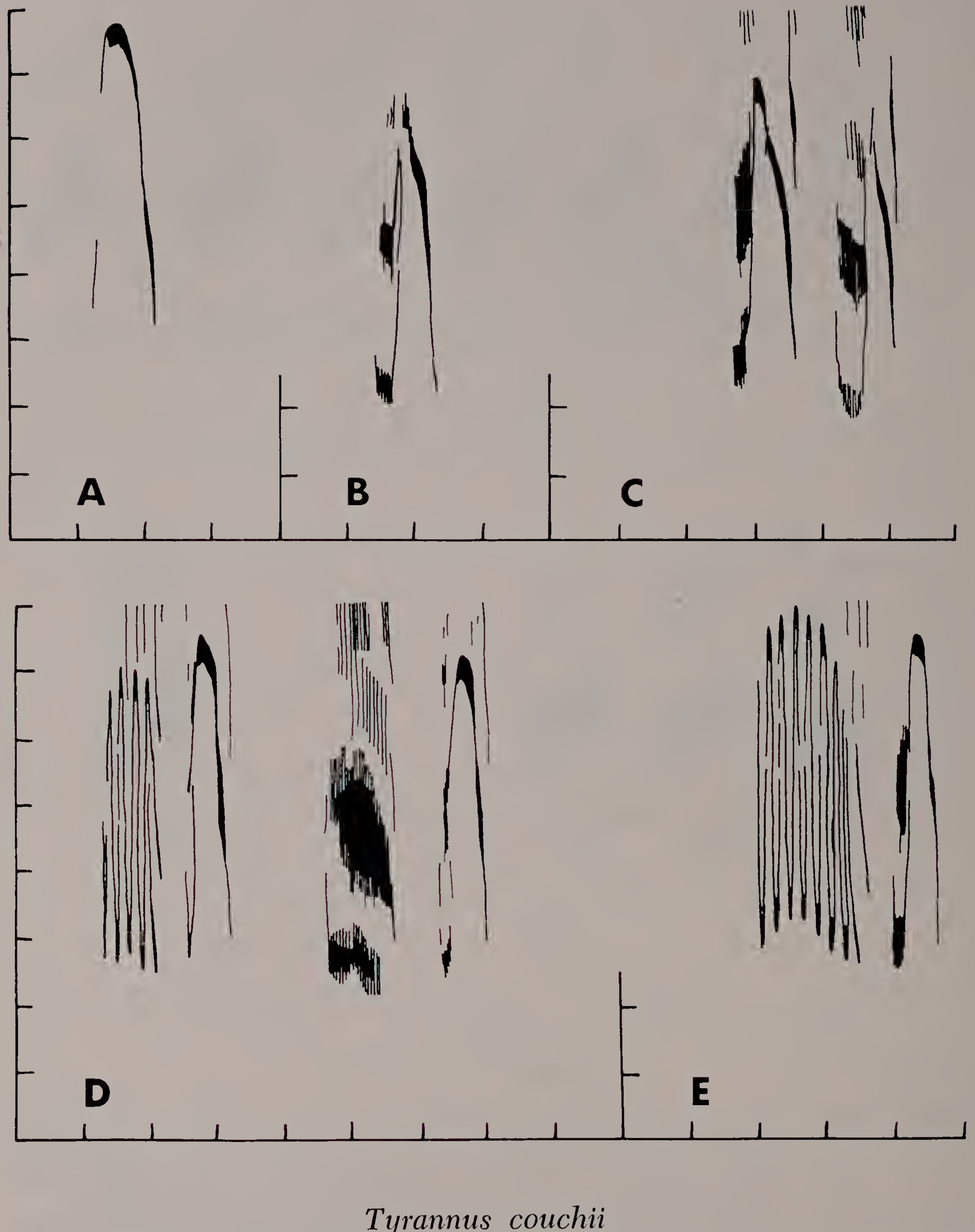
Tyrannus crassirostris

FIGURE 5:4a. RRV.
5:4b. One of the longer faint calls interspersed in the RRV calling of this individual.



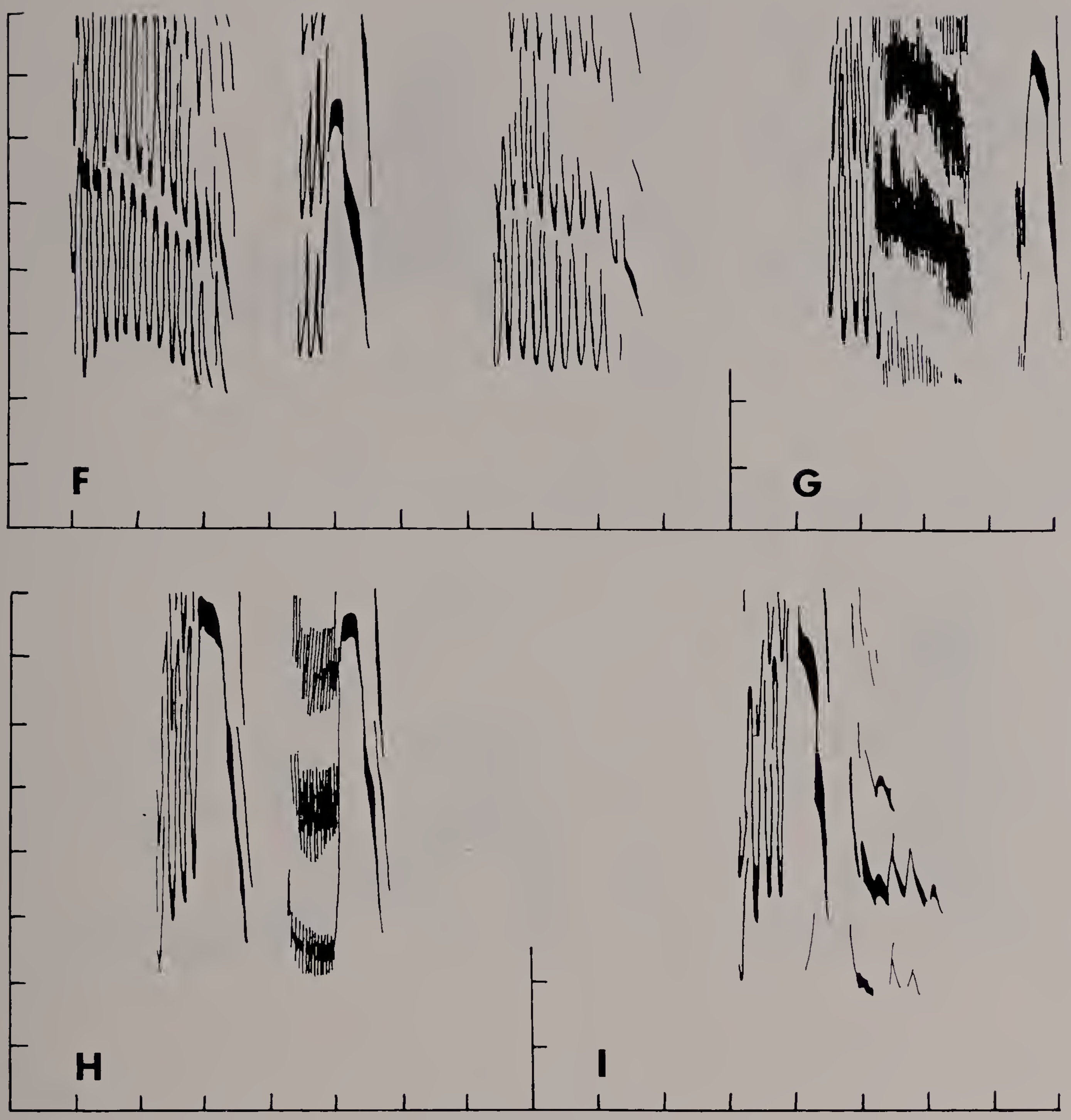
Tyrannus couchii

FIGURE 5:5a. LHV uttered by male as mate returned to nest while he was guarding (her call not shown).
5:5b. Three consecutive units from a greeting that became a fight when three individuals arrived at the nest nearly simultaneously.
5:5c. A single three peaked unit (with a Bill Snap before and after) uttered during subsequent fighting between two of these three individuals.



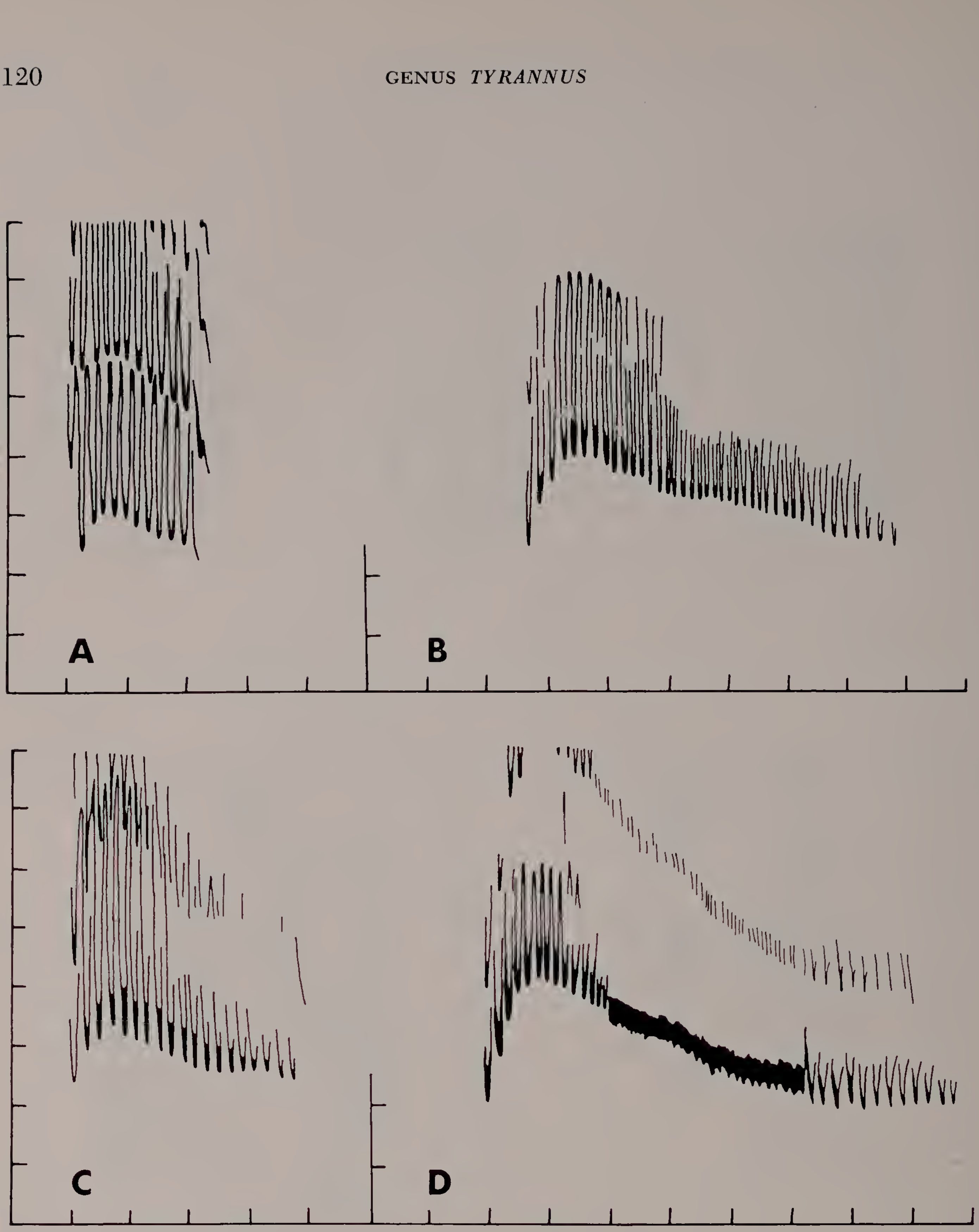
Tyrannus couchii

FIGURE 5:6a-e. Examples of female LHVs; (a) was given alone (while mate called), (b) was one of a series of similar simple units, (c) was a couplet of the sort which is repeated at times during greetings, (d) and (e) were given by a female who had just left her nest and landed with WFt on a nearby perch.



Tyrannus couchii

Figure 5:6f-i. More examples of the calls this female uttered with WFt after leaving the nest.



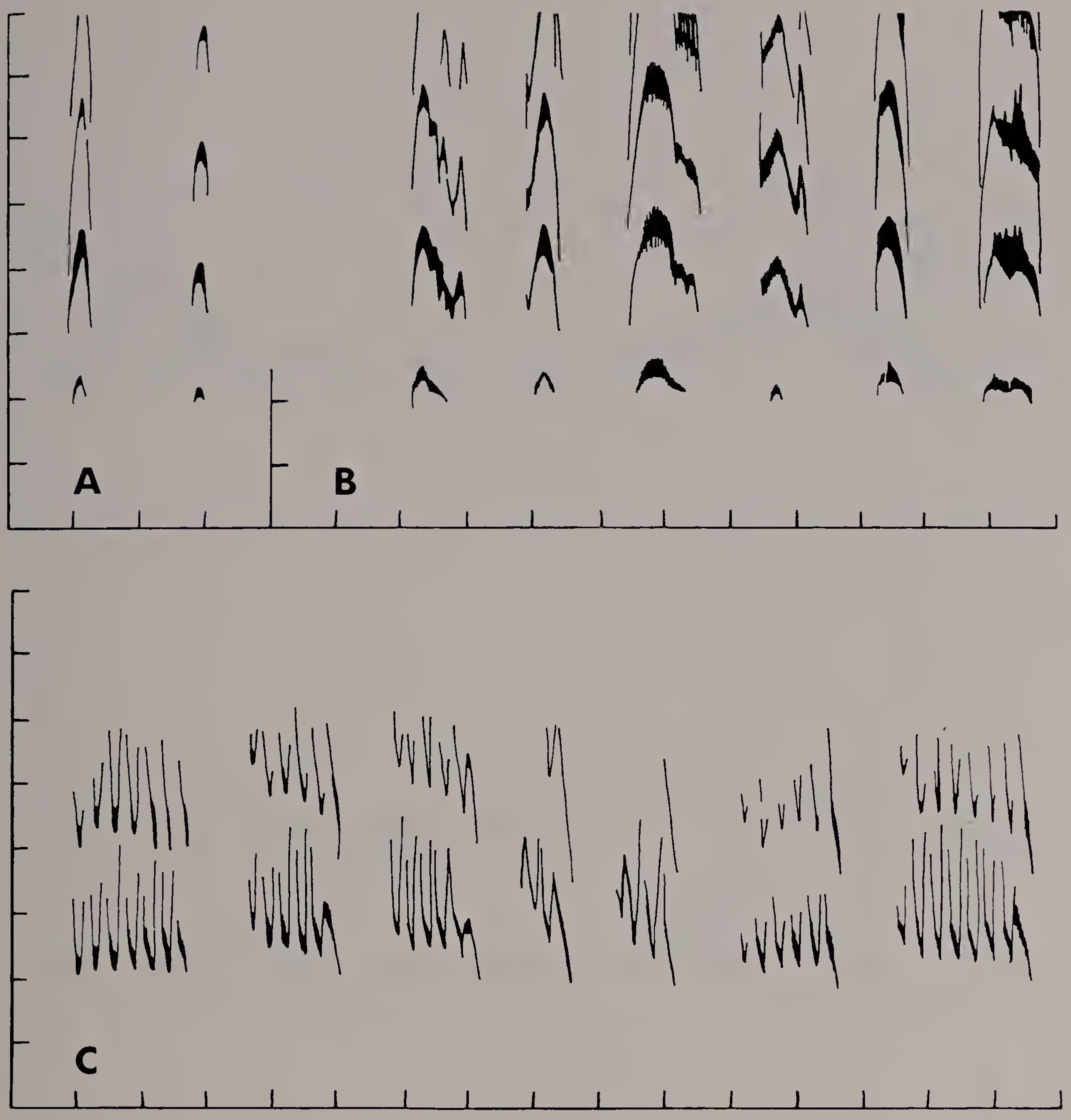
Tyrannus couchii

FIGURE 5:7a. Brief RHV uttered in flight, shortly before landing, by *T. couchii.*

5:7b. CdV uttered by a male perched alone 100' from the nest (but probably guarding); he remained there for some minutes, calling occasionally.

5:7c. RHV by female on landing on her perch after leaving nest where she had called ILHVs while working. Note that this is more prolonged than (a).

5:7d. CdV by a bird perched alone in the nest tree and repeating the call (after an agonistic encounter with some other conspecific).

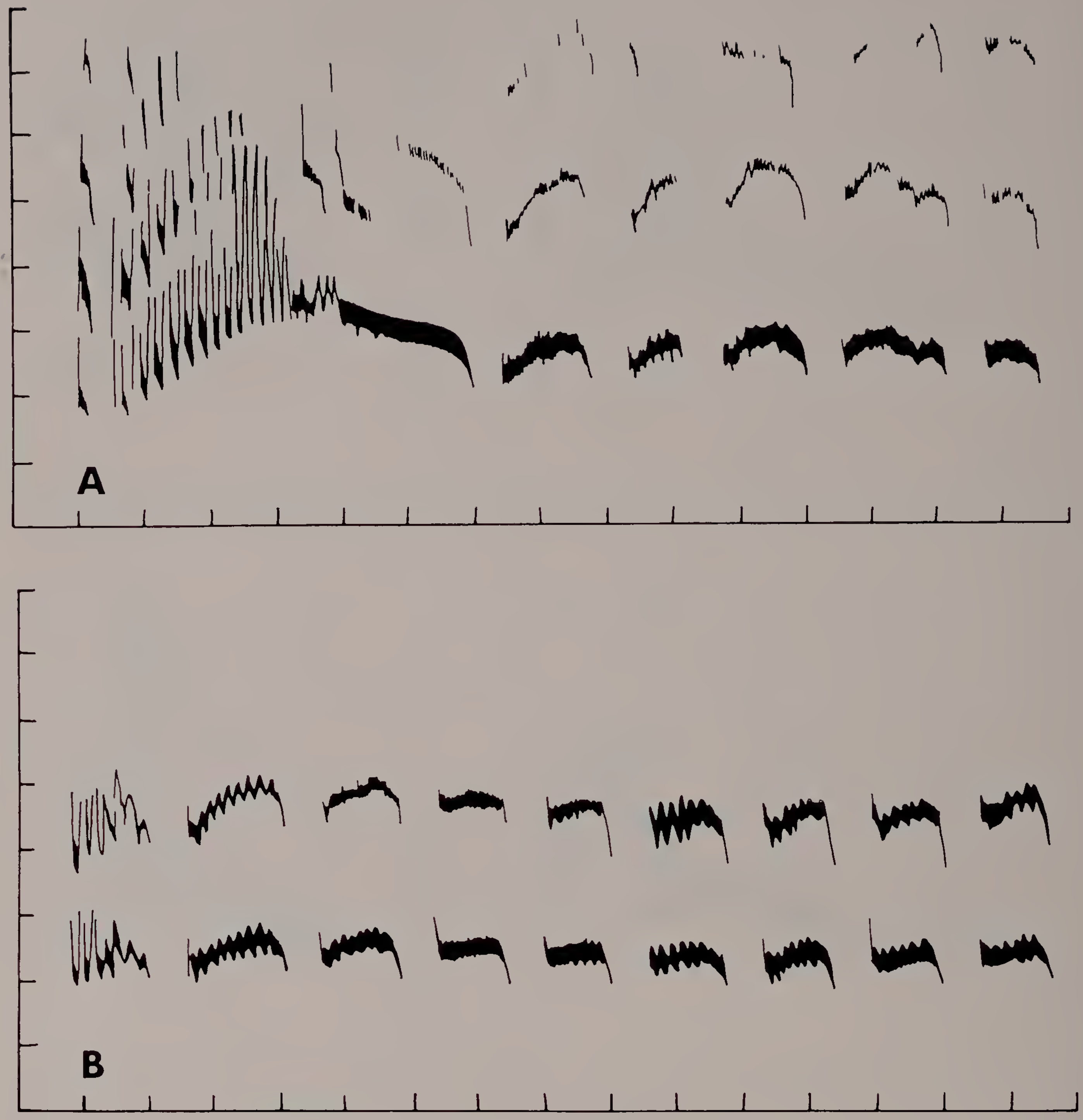


Tyrannus couchii

FIGURE 5:8a. Two examples (not consecutive) of ILHV, showing range of frequency.

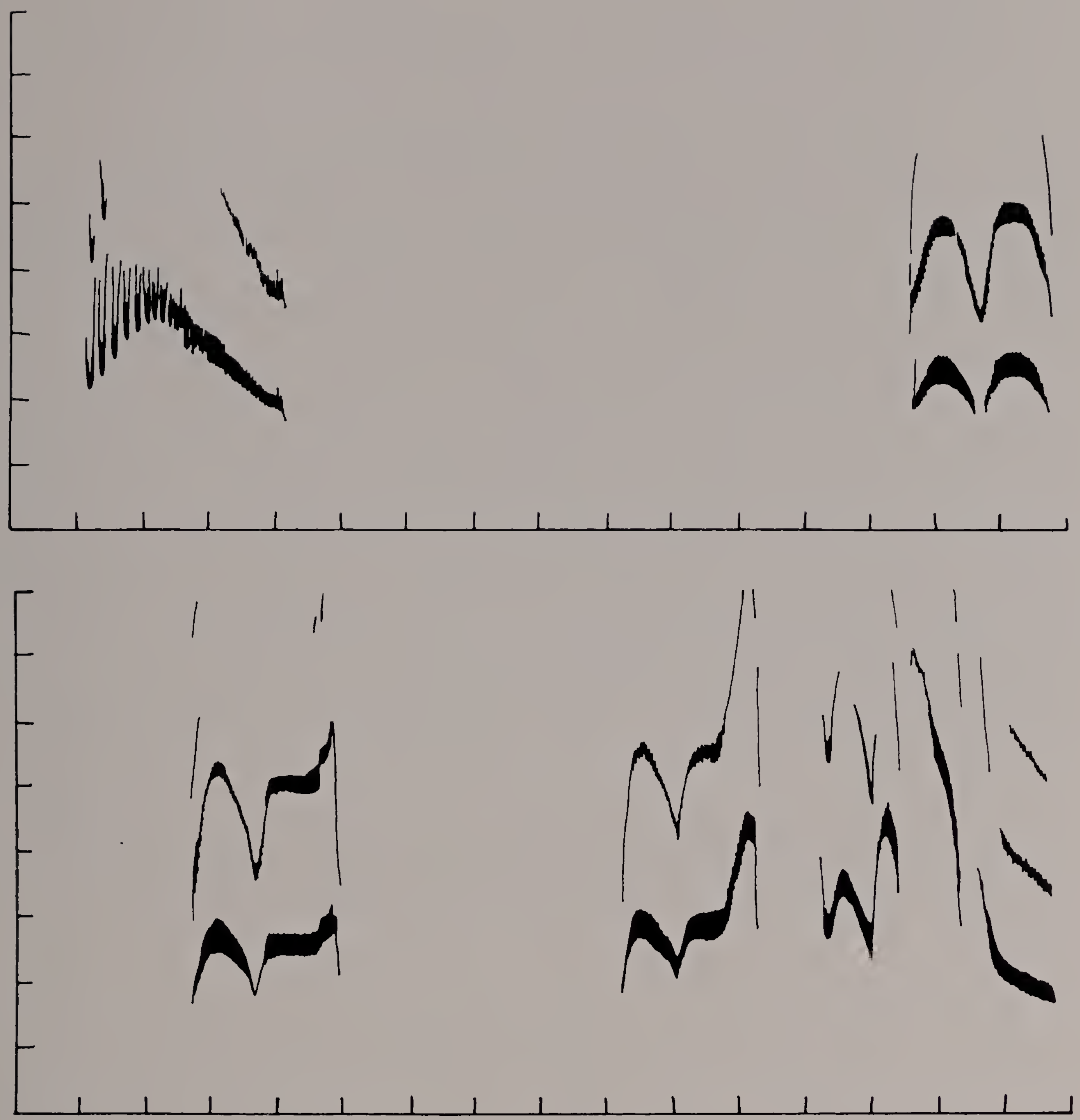
5:8b. A consecutive series of highly irregular ILHVs during a face-to-face fight between a defender and an intruder.

5:8c. Part of a CV burst (not from start) by a female working in the nest—usually she moved noticeably before each burst.



Tyrannus couchii

FIGURE 5:9a. Beginning of a prolonged CV by female in nest.
5:9b. A portion from the same CV, 1.8 seconds later than (a).



Tyrannus couchii

FIGURE 5:10. A fairly brief example of an RRV; 0.1 seconds have been deleted between the two lines.

Chapter 6.

CENTRAL AND SOUTH AMERICAN SPECIES

TYRANNUS MELANCHOLICUS, TROPICAL KINGBIRD

The Tropical Kingbird is the most brightly colored member of the genus. It has an olive-green back and bright yellow belly. The tail is olive-brown, lacks any pattern, and is slightly forked. The head is gray, although the throat is light or in some subspecies, white; a thin black mask extends from the bill through the eyes and onto the ear coverts. The concealed crown patch is bright vermillion. In plumage pattern, coloration, and size, males and females are essentially identical. Geographically this is the most widespread species, found in suitable habitat from extreme southwestern United States south to the Rio Negro in central Argentina. It has both migratory and non-migratory populations. The latter predominate and are the only ones I have studied to any extent. Skutch (1954, 1960) has observed that at high altitudes in Guatemala the species forms small wintering flocks, but that in Costa Rica "it remains paired, and in close contact with its breeding territory, throughout the year." It seems quite possible that in all of the sedentary populations both territories and pair bonds are maintained.

My observations of this species have been made primarily in Panama and the Canal Zone during May to early August, 1959, and February to April, 1962. I have made much less extensive observations, usually in or near the breeding season, in the Guayaquil region of Ecuador (1962), the lower Rimac valley of Peru (1962), the Argentine provinces of Buenos Aires, Tucumán, Salta, and Jujuy (1962), the Brazilian states of São Paulo, Minas Gerais, Pará, and Amazonas (1963), the Brazilian territory of Amapa (1963), the Georgetown region of British Guiana (1963), and the island of Trinidad (1963). Finally, a few birds of Mexican populations were seen and heard in post-breeding seasons in the states of Sonora (1962) and Veracruz (1964). In addition to my field experience, I have benefited from hearing tape recordings made in Venezuela by Paul Schwartz and by W. W. H. Gunn, and other recordings made by L. I. Davis in the Mexican states of Veracruz and Chiapas and deposited by him in the Cornell Library of Natural Sounds.

Details of the life history have been described by Skutch (1960). In most of its major features it does not differ significantly from that of the Eastern Kingbird, at least as regards the functioning of the display system at the level described below. This is with two important exceptions, however. (1) In the sedentary populations the formation of territories and pair bonds are relatively rare events, and are probably not limited to the period immediately preceding the breeding season. (2) Further, the season available for breeding is relatively prolonged, although each pair apparently takes advantage of it only once per year. In these sedentary populations inter-pair territorial squabbles are rare (I have never seen any interaction I could be sure was of this sort), and patrolling activities are rare (presumably a male who has lost his mate or who is just staking claim to a territory might patrol) or at least hard to recognize. The general level of social activity within the season also tends to be quite low relative to that of, say, *T. tyrannus* or *T. dominicensis,* perhaps because there is no need to initiate nesting at the beginning of the suitable season and because (in the populations with which I have worked) there are few or no pairs near enough to stimulate any given pair by their activities.

Despite frequent experience with Tropical Kingbirds I do not know many features of their display repertoire as well as I do the homologous features in the Eastern Kingbird. There are several reasons for this. The most important is that the vocalizations are not easily grouped into discrete categories, and are composed mostly of very brief, high pitched, thin sounding elements repeated in very rapid succession. These are very difficult for the human ear to follow, and particularly in the field it is difficult to distinguish between certain vocalizations. At times I was hampered by a shortage of magnetic tape, and could not obtain as thorough a sampling as I desired. This has had the additional effect that I cannot yet define clearly the "dialects" which occur among the widespread segments of the species' population. For instance, when I arrived in Argentina it had been some months since I had encountered Tropical Kingbirds, and I failed to recognize by ear that elements of the local populations' vocalizations were more than slightly condensed (i.e., each unit was briefer); I allotted rather little tape to the species and only recently, when I made sonagram analyses did I learn the difference in some vocalizations of the Argentine dialect. Further, as mentioned in the preceding paragraph, I have not found Tropical Kingbirds as socially active as breeding Eastern Kingbirds in many situations, and consequently have heard and seen on the average much less displaying. Finally, in any region in which I studied Tropical Kingbirds there were also numbers of other species of flycatchers which were important within the framework of my comparative approach, and the kingbirds received only a portion of my time. This dividing of my attention interfered more with my studies of this species than it did with any other kingbird. It will take a larger tape-recorded sample than I have at present to enable proper description of the vocalizations, and the following account must be taken as provisional.

Locomotory Hesitance Complex of Vocalizations

As in other species, an exchange of displays often happens in greetings between mates. A male will almost always Wing Flutter and utter a prolonged call in which a long, simple element is followed by a string of relatively shorter, simple ones (fig. 6:1a) sounding rather like "teee teeteeteeteeteeteeteeteeteetee." Compared to other calls, in the repertoire of this species, all of the elements in this series are usually relatively prolonged and slightly harsh. His mate will usually reply with a Wing Flutter and shorter series, often similar to the form he used. Often her call is much shorter, a burst of about four elements; in these instances, some of the elements (usually the last two, fig. 6:1b) may attain quite high peaks — a feature which I suspect is comparable to the inter-gradation with AeV in the terminal portions of brief LHVs of female *T. tyrannus* in some greetings. Sometimes females utter quite prolonged LHVs which are highly variable and contain various high-peaked elements. Other uses of these vocalizations also support their interpretation as LHVs. They may occur when a male is following his mate (fig. 6:1b); and the longer one, or something very much like it, is used by fledglings following their parents.

In a relatively prolonged greeting, the male may repeat his LHV several times, but the repetitions are always much briefer series than the first. They may, in fact, often be as short as a prolonged element and two somewhat shorter ones, but these still associate with the WFt and appear to be LHV forms rather than ILHVs. The prolonged LHV which these short bursts follow is often "concave" — that is, it begins loudly and decreases in both pitch and frequency before rising again in both in its terminal portion. Other prolonged LHVs may show nearly no change in frequency, or may slope slightly downward. LHVs of intermediate length may be used at times when a bird flies toward its mate and takes a perch while still 50 to 100 feet away.

In a pursuit of a Tropical Screech Owl (*Otus choliba*) in Argentina, a kingbird first called harsh "tee" elements in series of more-or-less LHV form, then began to modify these to have up to three abrupt peaks (fig. 6:2a) on closing with the owl. The use of multiple peaking suggests intermediacy with the RV, but also suggests the variations of LHVs of the western and Mexican species which occured in aggressive encounters. I have often watched *T. melancholicus* males attack large birds (hawks, toucans, even a frigate bird) which passed over their nests, and have sometimes heard a vocalization which sounded like "tee teetee" used as the kingbird swerved upward from its swooping attack. Unfortunately, without recordings it is impossible to know whether these were brief LHVs or RVs. Occasionally I have heard a bird use harsh calls as it flew toward a passing predator — these were probably quite similar to the calls recorded from the bird attacking the owl.

Incipient Locomotory Hesitance Vocalization

Tropical Kingbirds of either sex at times utter a vocalization which comprises a series of elements briefer than any of those customarily found in an LHV, and lacking any initially prolonged element. The series usually varies from about four to eight elements when all are of the same sort (fig. 6:2b) but may be extended to at least 16 elements (fig. 6:2c) when harsh elements are added at both ends; series of intermediate lengths usually have harsh elements only at the start. The "shape" of an ILHV differs markedly from that of an LHV — it is not concave but convex, with frequency at first increasing and then decreasing. The display intergrades with female LHVs, and perhaps with the RV.

I have often recorded this form from perched individuals which were warily watching my approach, and have occasionally recorded it during greetings. On at least two occasions in the Canal Zone, I have recorded it from an individual which was flycatching, nearly always when the bird was perched between flights, and sometimes just after it landed. I do not understand the significance of the longer series and the harsh elements, but they may indicate that the bird is more nearly in an LHV mood, or they may represent the Compound Vocalization of the species.

I have one recording which suggests an intermediate between the RV and this display, but which may just be a form of the ILHV used by juveniles. A lone, full-grown bird of the year was present for about two hours one afternoon where I was working near Santana, Territory of Amapa, Brazil. It kept uttering fairly constantly a single vocalization comprising one almost simple, prolonged element (fig. 6:3a) followed by a series of four brief elements, the whole having the frequency pattern of an RV rather than an ILHV. The young bird once approached and begged from a passing adult, but was ignored.

Repeated Vocalization

The vocalization I take to be RV comprises a brief, ILHV-like series preceded by a prolonged, usually multipeaked element of higher frequency than the start of the series. The calls in my rather small sample are rather variable, but most *sound* like "tee teetee." The elements of the series are difficult to distinguish.

I have recorded only one male that was repeating a vocalization at intervals as he guarded near the nest in the absence of his mate. Of the nine calls in my sample, six are very similar (fig. 6:3b), and the other three have the same kind of initial element followed by three, four, and four elements in the series. Each of these latter series has a prolonged but simple element in the first or second position, making the vocalization appear to be related to an LHV.

Two samples were recorded from a bird which was (a) calling rarely from a perch in the early morning, post-RRV period, and (b) calling in the same general region in the late evening twilight. The early morning sample has only two calls, the first like most of the guarding male's calls (see above) but the second with many more multipeaked elements (fig. 6:3c). The evening sample has nine calls, of which the first five are similar (fig. 6:3d) and have the prolonged element preceded by a very brief introductory element. In the next two calls the prolonged element is shorter, then becomes simple and like the LHV form in the eighth, reverting to the original form in the last.

All of these cases seem to be variations on a theme, and all were being used in situations in which I should expect to encounter the RV or, although less likely, the CdV. So far as I am aware, this species has no call corresponding to the CdVs of other species unless it is the longer ILHV form with associated harsh elements. The evidence for this is extremely scanty.

Chatter Vocalization

The CV of *T. melancholicus* sounds much like that of *T. tyrannus.* It is a series of simple units, each much briefer than an LHV element (see fig. 6:4a). Females often utter the CV when apparently at least slightly nervous while nest building or nest site prospecting, and when visiting their nest to feed the nestlings in the presence of an observer.

A second form may occur in some circumstances in which a female uses a transitional stage between a prolonged LHV and a CV. I have several times been watching a nest when the female landed on a perch near the nest with LHV and WFt, and then went to the nest and fed the begging young, stopping the WFt and changing the vocalization to a fainter form which she maintained throughout the remainder of the visit. In such a case, the portion which seems to be a CV can be distinguished from the initial prolonged LHV only because the former is apparently composed of briefer units, uttered less emphatically. Not only is this sort of intergradation between CV and LHV apparently possible, but, as in other species, the CV can at times replace an LHV in a greeting between mates. When a female utters a relatively prolonged vocalization during a greeting, it is usually composed of briefer units than is the male's call; sometimes a female will change from an LHV to a CV during a greeting.

Regularly Repeated Vocalization

Description. In Panamanian Tropical Kingbirds the RRV typically has three phrases, although the first is sometimes omitted. The first and second phrases are closely similar, each usually comprising a relatively long element followed by three (occasionally just two) briefer ones. Brief, stuttering, often harsh introductory elements sometimes precede the first or both of these phrases. The third phrase is much the most complex. It begins with a relatively long element followed by two briefer ones (i.e., essentially a phrase one or two) and then a very brief, abruptly ascending element which reaches as high a frequency as any part of the vocalization (beginning or ending elements of phrase three may be as high). This is followed by three to five brief elements, all but the last of which are usually bipeaked (see fig. 6:4b). The patterning of the elements of the three phrases heard in succession sounds like the starting of a balky gasoline engine.

Recorded samples demonstrate inter- and intra-individual variation in the number of phrases, in a tendency to run the first two together into one, in the total length of the display, and the number of elements in phrases one and two. Phrase three is relatively constant in the number of elements used by any one individual, but varies in duration; while it varies geographically it is more consistent than the others. Among individuals there seem to be consistent differences in various characteristics of the third phrase, but my sample size is too small to prove this. The meager sample suggests that in addition to intra-individual and inter-individual variations, there are differences between populations. It would not be safe to attempt to generalize at this stage, but it does appear that all three phrases may show dialect peculiarities. Some differences of all phrases appear to characterize birds I have recorded from southern Brazil and central and northwestern Argentina as distinct from birds from Panama, Venezuela, and Trinidad. In no case, however, have I heard or recorded an RRV from a Tropical Kingbird that would not permit me to recognize the species immediately.

Use. As in the Eastern Kingbird, the RRV is a display of males in the predawn twilight. I have heard it at no other time of day, nor has Skutch (1954). Low light intensities are of shorter duration in the tropics and subtropics than in the North Temperate Zone where the former species breeds, and on cloudless mornings Tropical Kingbirds have just begun to sustain a good rate of regular repetition when they begin to introduce irregularities, and the period of RRV calling comes to a close. Skutch comments that there is seasonal variation in its usage, some birds starting early in or before the breeding season, some continuing after the season is largely over. I have also found that within a space of a few miles there may be much or little calling at different sites, and some males may not use the RRV calling in localities where population densities are relatively high. The irregularity with which the display is used has caused me to miss it at some localities; for example, none of the birds with which I worked in Buenos Aires Province, Argentina, used it during the several days I was there in early spring, although other species such as the Fork-tailed Flycatcher were using their homologues, and I was able to hear and record it from other Tropical Kingbirds elsewhere in Argentina.

Tumble Flight

I have known only one individual Tropical Kingbird to perform what I believe to be the TF display. It did this twice in the three days I was camped near its territory in southern Tucuman, Argentina. Both occasions were crepuscular, first in the late evening twilight on 16 November, 1962, and next in the early predawn twilight the following morning, before the RRV was begun. In both cases the flight was rapid and twisted erratically, and the bird kept just above the tops of the trees. (This form is one extreme of the range of variation of the homologous display in *T. tyrannus.*) In the dense thorn forest vegetation and extremely low light intensities it was impossible to see either flight in its entirety, but there were no true "tumbles" in what I could see. Throughout both flights the bird repeated over and over brief bursts of "tee" calls.

The absence of Tumble Flights is especially surprising because I have spent much time with Tropical Kingbirds in the crepuscular periods when other kingbird species often perform their homologues of this display. Further, I have seen Tropical Kingbirds chase many hawks, toucans, an owl, and other possible predators, without using the TF as the kingbird returned from any chase.

I am inclined to accept the Tucuman observations as indicating that a flight display does occur in this species, possibly without actual "tumbles." At least within the situations in which I have observed Tropical Kingbirds it is obvious that the display is rare. Yet I have never worked in a region where the population density of the species was great enough to bring many individuals into contact. I have never, in fact, seen a clearly recognizable territorial encounter. It remains an open question whether or not the TF will be found to be more frequent (and possibly seen with tumbles) should a denser breeding population be found.

Crouch, Revealed Crown Patch, Raised RCP, and Crown Ruffled

The only example of full Crouch which I have seen appeared in all respects identical with the homologous display in *T. tyrannus.* It was given by an individual which I think was a territorial intruder at a time when another conspecific had landed nearby and was nearly facing the first. The individual in the Crouch faced directly *away* from the other, which gave an RRCP, and both called repeatedly, using brief vocalizations (distance contributed to my usual difficulties in recognizing calls). Both individuals stopped displaying within a few seconds, and within a minute the one who had Crouched flew off. On a very few other occasions I have seen partial Crouch postures (usually lacking the feather ruffling); one was directed toward a Clay-colored Robin (*Turdus grayi*), and accompanied by a "tee teetee" call (probably an RV); another was given silently by one kingbird just after it had supplanted a conspecific. As in some other kingbirds, I also saw a case in which this display intergraded with a WFt and LHV display. In this instance a pair of Tropical Kingbirds, in which the female was feeding nestlings, became very excited as the male approached his mate near the nest. Both used the WFt and LHV, and the female oriented at right angles to the male, gradually assumed a full Crouch posture with attendant feather ruffling, but continued to use the WFt and LHV. The male did not modify his display and continued to face his mate; she next used the RCP and he immediately followed suit. Then she flew off and he followed.

In the two observations mentioned above, the RCP and RRCP appeared identical with their homologues in *T. tyrannus*. Skutch (1954) has seen the RCP used by a female uttering a CV as she came alone to her nest in which she had not yet laid; I suspect this was in response to his presence (or the presence of his blind).

Crown Ruffled is the only additional plumage erection display on which I have made any appreciable observations. It, too, seems closely similar to its homologue in *T. tyrannus*.

Gape and Bill Snap

I have not observed Gaping in adults of the Tropical Kingbird, although I suspect this is only because I have seen so few aggressive encounters. I have seen nestlings Gape with Crown Ruffled, and direct the gaping toward me as a threat display. Tropical Kingbirds attacking predators do sometimes use the Bill Snap display.

Displays Using Wing and Tail Movements

The Wing Flutter seems to be essentially as in *T. tyrannus* in form and usage. The tail is spread, and there is a simultaneous Tail Quiver. One form difference is that the wings are usually held well above the back when the display is vigorous, although barely above the back in less vigorous instances. An observation made in Panama provides a clear demonstration of a function of this and accompanying displays. One member of a family was behaving aggressively and attacking all of the others, one at a time. One of the birds being attacked always faced the attacker with the WFt and spread tail, and gave an LH Complex call (a series of "tee" units with the first two or three emphasized). In each case the attacker started toward it, then passed by and attacked one which was not displaying, or which displayed only very weakly before fleeing. Eventually, all but the one which always began to display vigorously at the first intention movements of the attacker were chased away. This one was always able to get what Moynihan (1955b) has called an "exemplary display" effect — the attacker, when it approached, would land by the displaying bird, display in kind, and they would then stay perched quietly near one another. The morning was so overcast I was unable to determine from the color of the underparts if these were the two adults of the family; probably they were, and a factor of individual recognition must have entered into the event.

Again as in other kingbirds, aggressive individuals may use a Wing Flick display. This is done while fanning the tail open and shut, but I have yet to observe a Tail Flick (sample size quite small).

Displays of Nestlings and Fledglings

Nestlings have a thin call uttered during begging, usually repeated in series. Before fledging they develop a "tee teetee" call, with emphasis on the first unit; it sounds much like one of the adult calls and is used persistently. This is additional evidence supporting the interpretation of the similar sounding call of the juvenile discussed under ILHV as comparable to the ILHV of *T. tyrannus.* Fledglings develop a prolonged LHV with WFt, possibly from the series of begging calls. Nestlings near the age of fledging will call "tee" and "tee teetee," Gape, and give a Crown Ruffled toward an observer who disturbs them in the nest.

TYRANNUS NIVEIGULARIS, SNOWY-THROATED KINGBIRD

T. niveigularis is a slightly small kingbird, colored in general like a Tropical Kingbird, but with a pale gray back which contrasts with its black, unforked tail and quite conspicuous black mask, and even with its bright white throat. It has a restricted distribution west of the Andes in arid, subarid and in places seasonally quite wet coastal country from southern Colombia south to the Department of Ancash in Peru (the southernmost Peruvian site, 9°53′S, is from Koepcke, 1961, p. 17). I have studied the species in Ecuador, but only briefly, for a few hours on the mornings of 28, 29, and 31 January, 1962, near Guayaquil, and during the late morning and early afternoon of 30 January, 1962, about 80 kilometers north of that city near Balzar. Both sites were in semi-wooded agricultural and second-growth land in what probably had been a monsoon forest region. At each site I had a single pair, and both pairs appeared to be in the pre-nesting phase of their annual cycle, although the rainy season was well begun.

Locomotory Hesitance Complex of Vocalizations

When one member of either of the two pairs flew toward and landed near its mate, the birds would usually orient so as not to face directly, and utter calls which sound at least superficially like the calls *T. melancholicus* uses in similar situations. Several examples were tape recorded, and show that each individual of a pair used a call different from that of the other individual. Typically, both would utter a relatively long burst, then one to three shorter bursts, then cease calling — the common greeting pattern of the genus at this stage in the annual cycle.

The vocalizations of one individual were longer than that of its mate, suggesting that the former was the male. A typical series ranged from about six to 17 or more units, began with one or more very brief units, switched to three or four more prolonged, chevron-shaped units which were relatively the loudest part of the series, and then to a few similar units, truncated as they peaked (fig. 6:5a). Sometimes a series would go on to return to the non-truncated form and then revert back to the truncated.

The other individual used only extremely brief units in series of up to at least ten, but usually in short bursts of three to five (occasionally just one toward the end of an incident). These were quite simple ascending notes, with the greatest concentration of energy initially, at the lowest frequency (fig. 6:5b).

A Brief Vocalization

When perched between foraging flights, or perched near its mate, one individual would give occasional brief, simple "teek" calls (about 0.02 seconds, see fig. 6.5c) of lower pitch than the LHV. I recorded them from both pairs, and never heard more than one uttered at a time, with long intervals between. Presumably this "teek" is either an ILHV or an RV.

A Flight Display

After locating the Balzar pair of Snowy-throated Kingbirds, I stood in the open and watched them for about an hour, as they perched in the top of a large tree in the midst of semi-open second growth, made occasional foraging flights, and called and behaved as did the Guayaquil pair. Then I began to approach the tree, and, as I walked forward, one of them flew toward me and began displaying. Its wings were held stiffly horizontal and fluttered rapidly, and it maintained a horizontal flight or climbed just slightly. It repeated a complex phrase (fig. 6:5d) four times, quite rapidly, then, having passed over my head, made a wide circle, flying normally, and returned silently to its perch where it settled and remained silent for several minutes before flying off to forage elsewhere.

I have observed similar circling flights in at least *T. tyrannus* that seemed to be directed toward me, and which, judging by their vocalizations, were forms related to the Tumble Flight, although no tumbles occurred. It is significant that so complex a phrase was used, as I have recorded the full complex portion of the RRV from *T. verticalis* and *T. forficatus* in Tumble Flights (the calls recorded from *T. tyrannus* in Tumble Flights often approach the form of the ultimate part of its RRV), and I have heard the RRV from *T. dominicensis* in an odd, fluttering flight involving two birds. Two conclusions thus seem probable: (1) *T. niveigularis* has a flight display at least somewhat like that of other *Tyrannus* species in which a display flight is known, but possibly (not by any means certainly) lacking the tumbling portion, and (2) at least the complex portion of the RRV of this species should closely resemble the call heard in this flight. I checked each morning for the RRV of my Guayaquil pair, and failed to hear it; they had no near neighbors, and the male may have been using it only rarely, if at all. The recorded phrase from the flight display, however, is closely similar in many respects to the RRV typical of the genus.

Other Non-vocal Displays

A WFt has been mentioned, used with the LHV as in other species of the genus. In appearance it is very like the WFt of *T. tyrannus,* and the displaying birds adopt postures similar to those of that species, whether in flight or perched. No other non-vocal displays were observed.

TYRANNUS ALBOGULARIS, WHITE-THROATED KINGBIRD

T. albogularis looks extremely similar to *T. melancholicus,* but is slightly paler on the back and much paler on the forehead and throat than most subspecies of *melancholicus,* including the one with which it is sympatric. The black mask seems fairly prominent, probably because of the pale forehead and throat. The chest lacks the tinge of olive found in *melancholicus.* Its bill is slightly narrower and shorter than that of the more widespread species. *T. albogularis* apparently inhabits all or most of the interior "cerrados" and at least some of the savannahs, of southern and central Brazil northward even to the isolated patches along the borders of southeastern Venezuela, British Guiana, and Surinam, eastward to the coastal savannahs of the territory of Amapa, north of the mouth of the Amazon, and westward into Peru. I found a few pairs on the edges of marshes in open cerrado country on both sides of the Rio Grande along a road between Barretos (São Paulo) and Planura (Minas Gerais). One of these pairs had fledglings, and was studied on 15, 16, and 17 January, 1963. Later, on 5 and 6 February, 1963, I observed a bird which did not display, in the savannah near Porto Platon, Territory of Amapa.

I learned little about the birds' displays. The tall marsh grasses made following them impracticable, exceptionally heavy rains ruined all of the early morning hours and interfered at other times, and it is always difficult to begin work with a new species shortly after their young have fledged. Fortunately, the young were still quite stubby-tailed, so that I was able to distinguish them easily from the adults. Thus I was able to study greeting displays between the parents, to record several examples of the LHVs exchanged, and to observe the Wing Flutter display both adults used. This WFT appeared quite like its homologue in other species of kingbirds. It is also sometimes used when the young and adults meet — the fledglings often approached their parents — but I was unable to obtain good recordings of the vocalizations exchanged then.

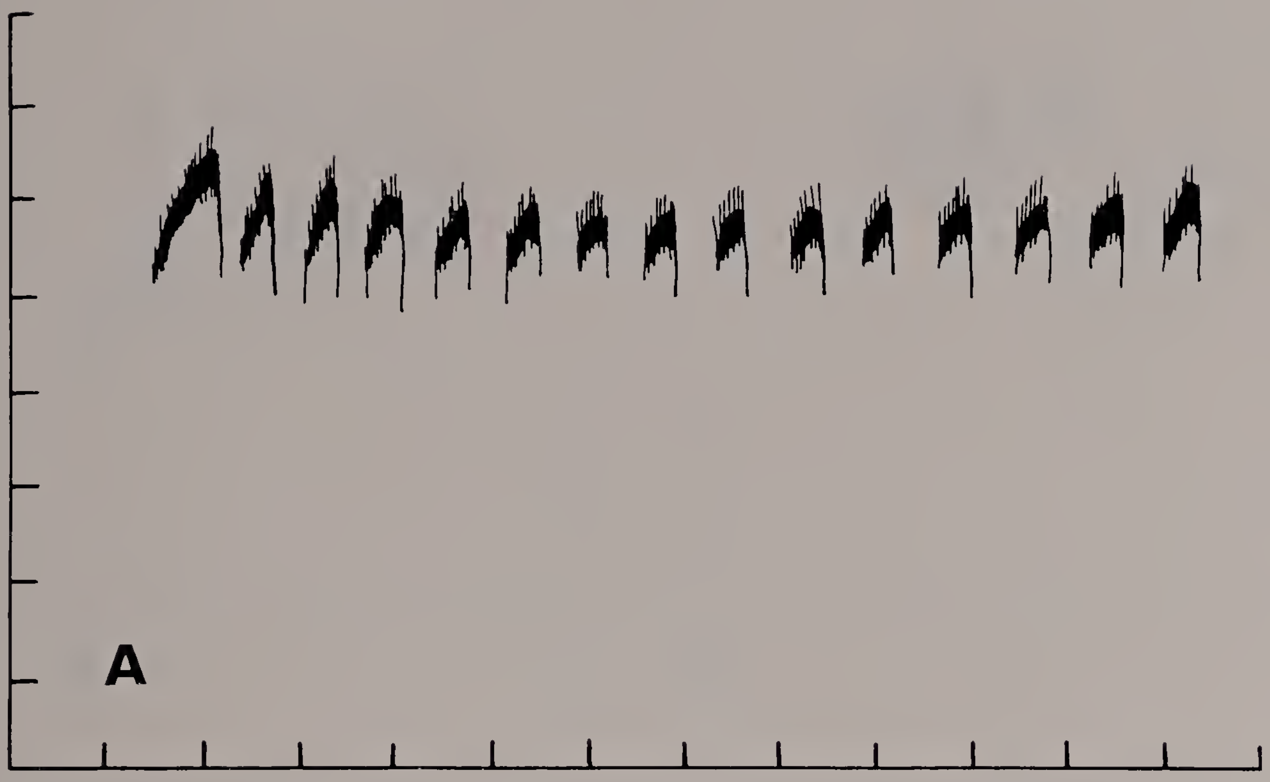
There are at least two forms of the LHV. One is relatively prolonged in most cases, rather harsh, and like a lower pitched version of the similar *T. melancholicus* form, although its overall "shape" is usually convex. It is used in greetings, and both sexes apparently utter nearly identical versions of it, although one tends to be relatively shorter and lower in frequency (probably used by the female). After a presumed male has given a prolonged version he may repeat a couple of much shorter ones which are essentially identical with it in all other respects (a four-element form is illustrated in fig. 6: 6a). The presumed female also has shorter LHVs she may use in greetings; these are less harsh (fig. 6: 6b) and sometimes have a high-peaked terminal element (fig. 6: 6c). Thus all of the known LHV forms are quite comparable to their homologues in *T. melancholicus.*

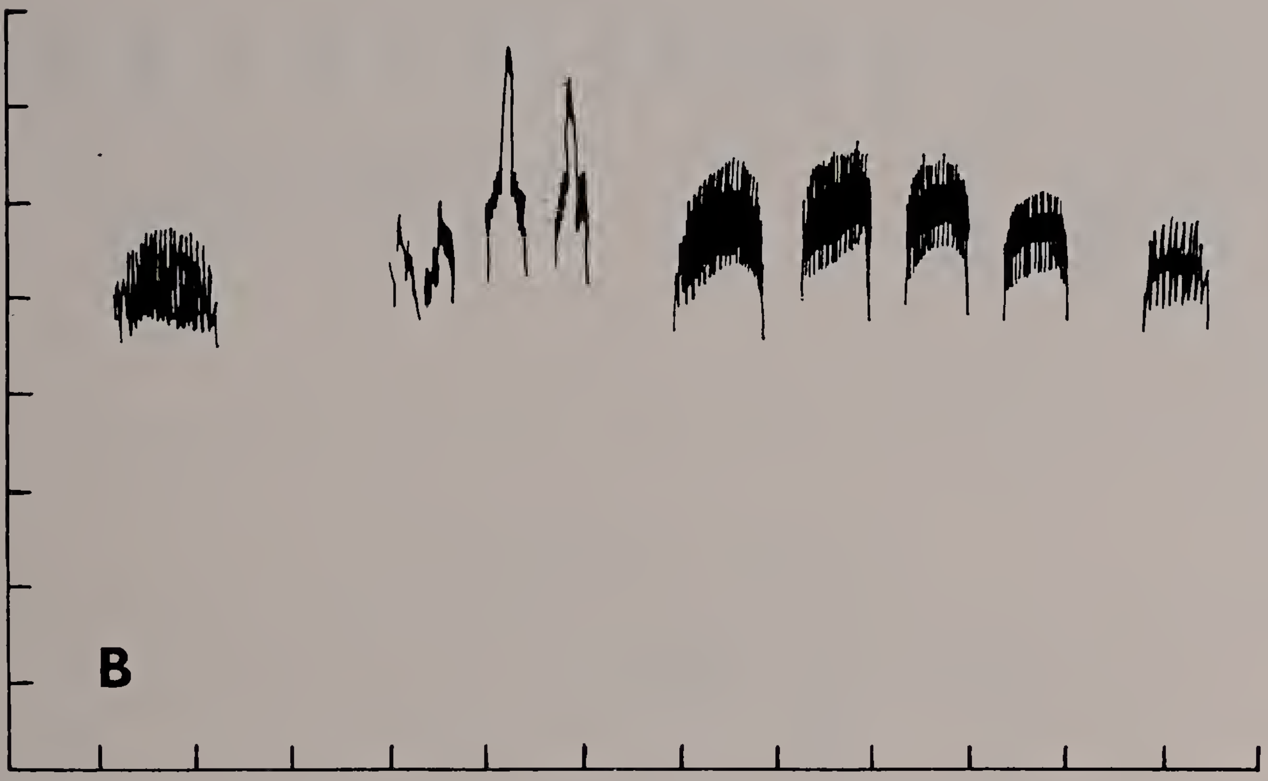
The second of the vocalizations is probably an Incipient Locomotory Hesitance Vocalization (fig. 6: 6d). This is a compact burst of brief units with a generally convex "shape" rather like the reverse of the similar *T. melancholicus* ILHV in that it reaches its highest frequency quickly and tapers off slowly. It is often given just before flying or while in flight, but is also uttered by perched individuals, especially if some other individual has just uttered a similar call. Brief versions of it occur in two of the greetings I recorded, apparently uttered by the presumed male in addition to his longer LHVs. I think, but am not sure, that it was sometimes used alone as a greeting vocalization; what evidence I have makes it seem very much like an ILHV.

T. albogularis also often uses a quite brief, single-unit call ("tch," fig. 6: 7a) which varies in frequency. It may be a Repeated Vocalization. This is sometimes repeated in short sets of two, three, or four units if a bird is calling frequently, and in these cases each component of a set is different from the other components (e.g., fig. 6: 7b, 7c). On the morning of 17 January, one of the adults became much agitated for several minutes, twisted and pivoted on its perch, and uttered a great many single calls, many brief sets, and some brief sets leading into what appeared to be prolonged versions of the ILHV. Under the circumstances, it would not be surprising if the latter were actually not ILHV but CdV (e.g., fig. 6: 7d) but I have no other case with which to support this idea. As the bird became less restive this vocalization dropped out as soon as the calling rate began to fall off, and well before the other vocalizations stopped.

The calls used by fledglings when begging from the adults were usually weak and recorded poorly, but appeared to be mostly of the broad "chee" variant (fig. 6: 6e) of the single call. Fledglings also gave more standard "tch" versions commonly, and used the probable ILHV.

FIGURES

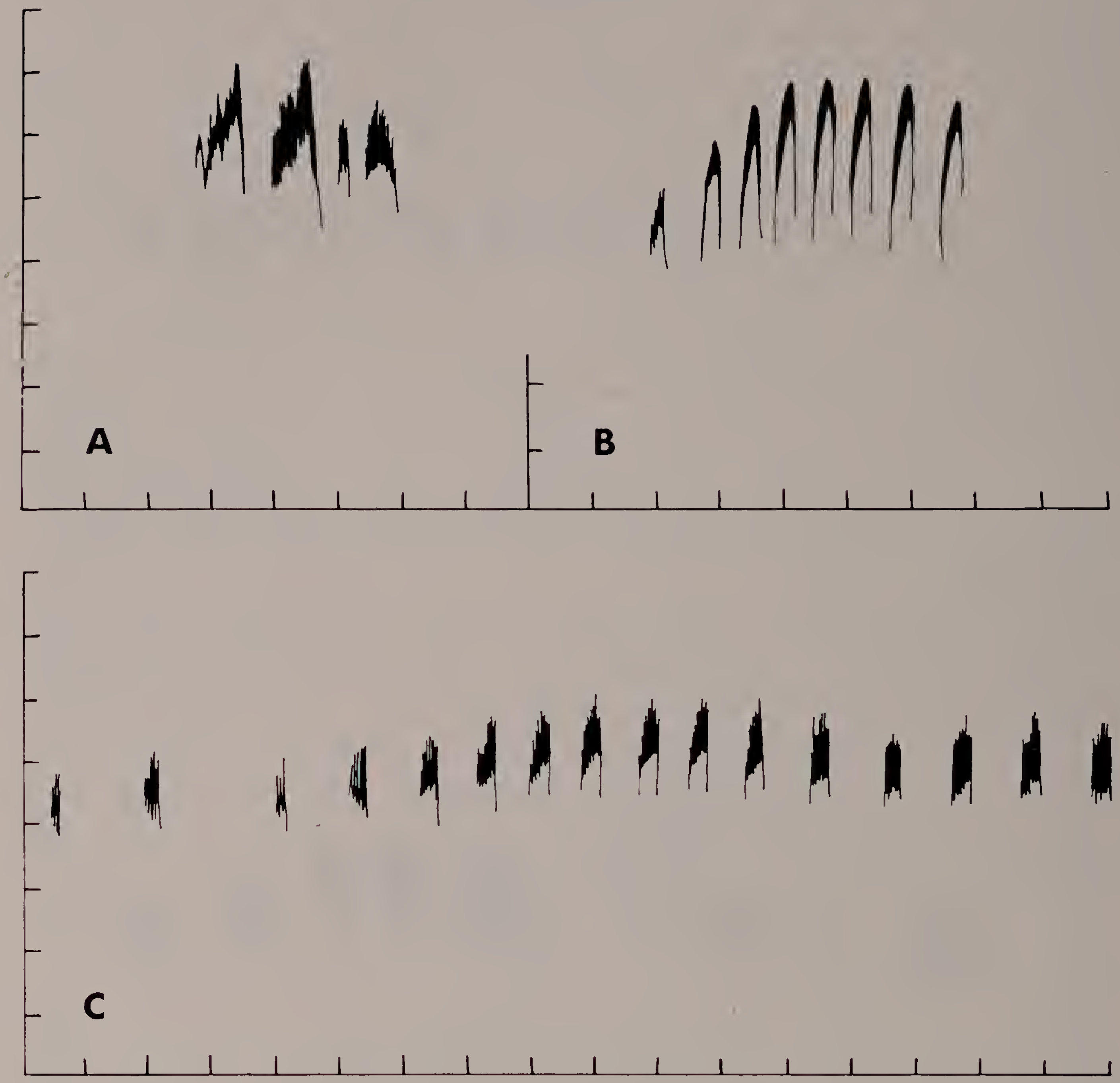




Tyrannus melancholicus

FIGURE 6:1a. A moderately prolonged LHV of the sort usually uttered by males (females have a closely similar form). Uttered by an individual on landing after flying toward its mate but stopping 50′ short (Panama).

6:1b. An exchange of LHV calls within a pair, one bird following the other. All of the harsh calls are by one individual, and the set of four brief elements (second to fifth in the illustration) is by its mate — probably the female (Argentina).

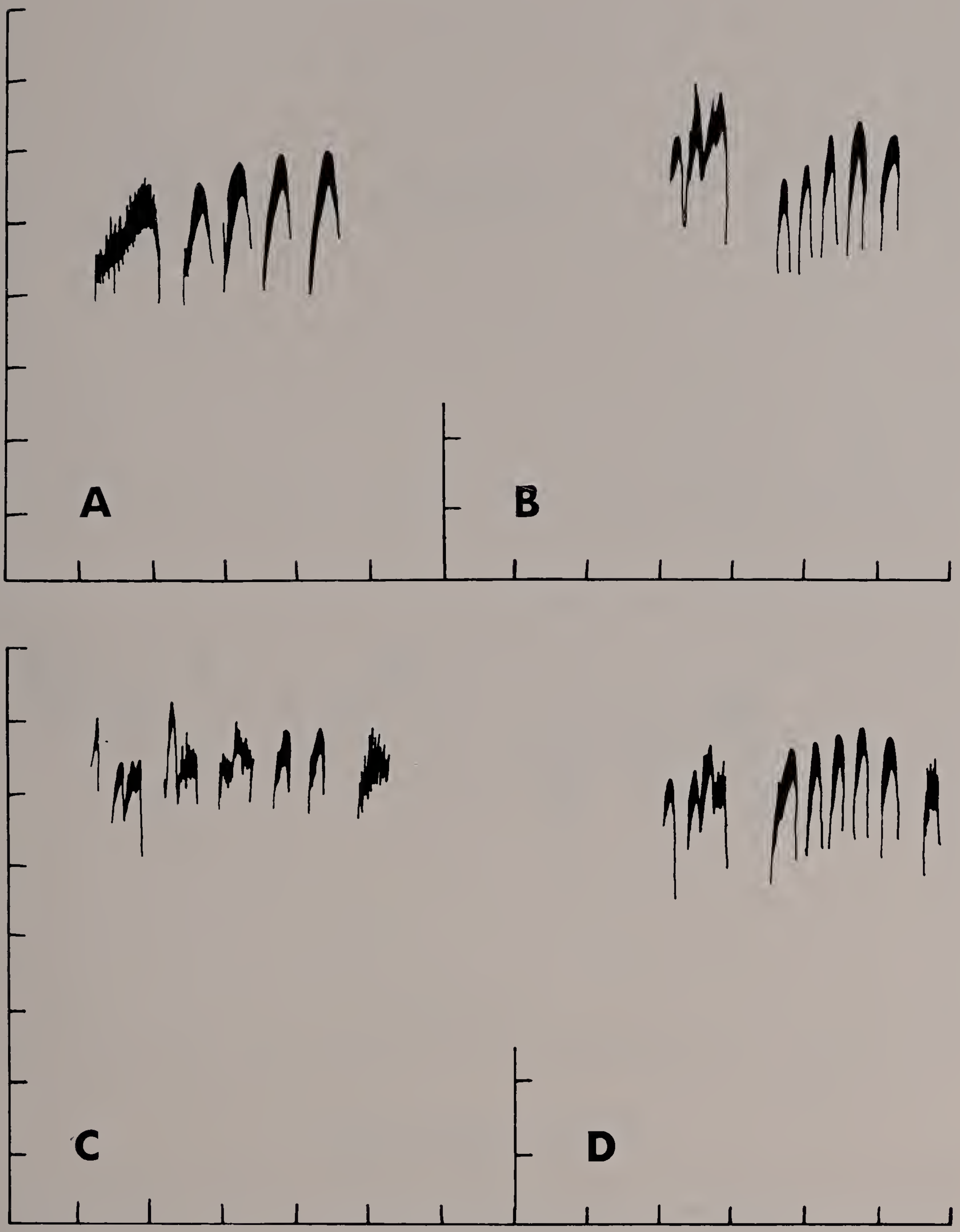


Tyrannus melancholicus

FIGURE 6:2a. One of the shorter bursts of calls uttered by a Tropical Kingbird pursuing an owl (Argentina).

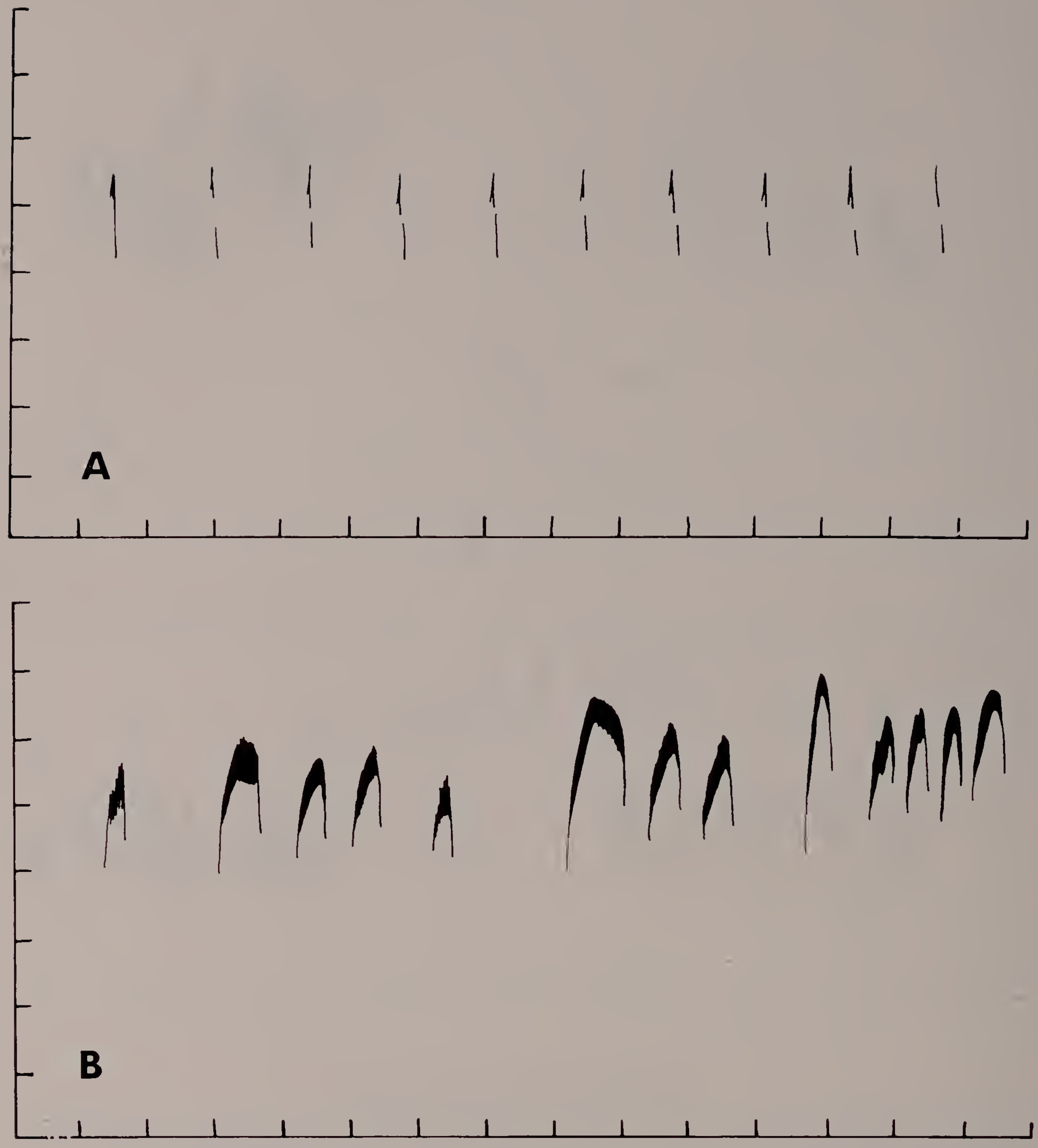
6:2b. ILHV by a bird perched between flycatching flights, alone (Canal Zone).

6:2c. Prolonged ILHV-type call by a bird perched between flycatching flights, about 100′ from its mate and with another pair visible in the distance (Canal Zone).



Tyrannus melancholicus

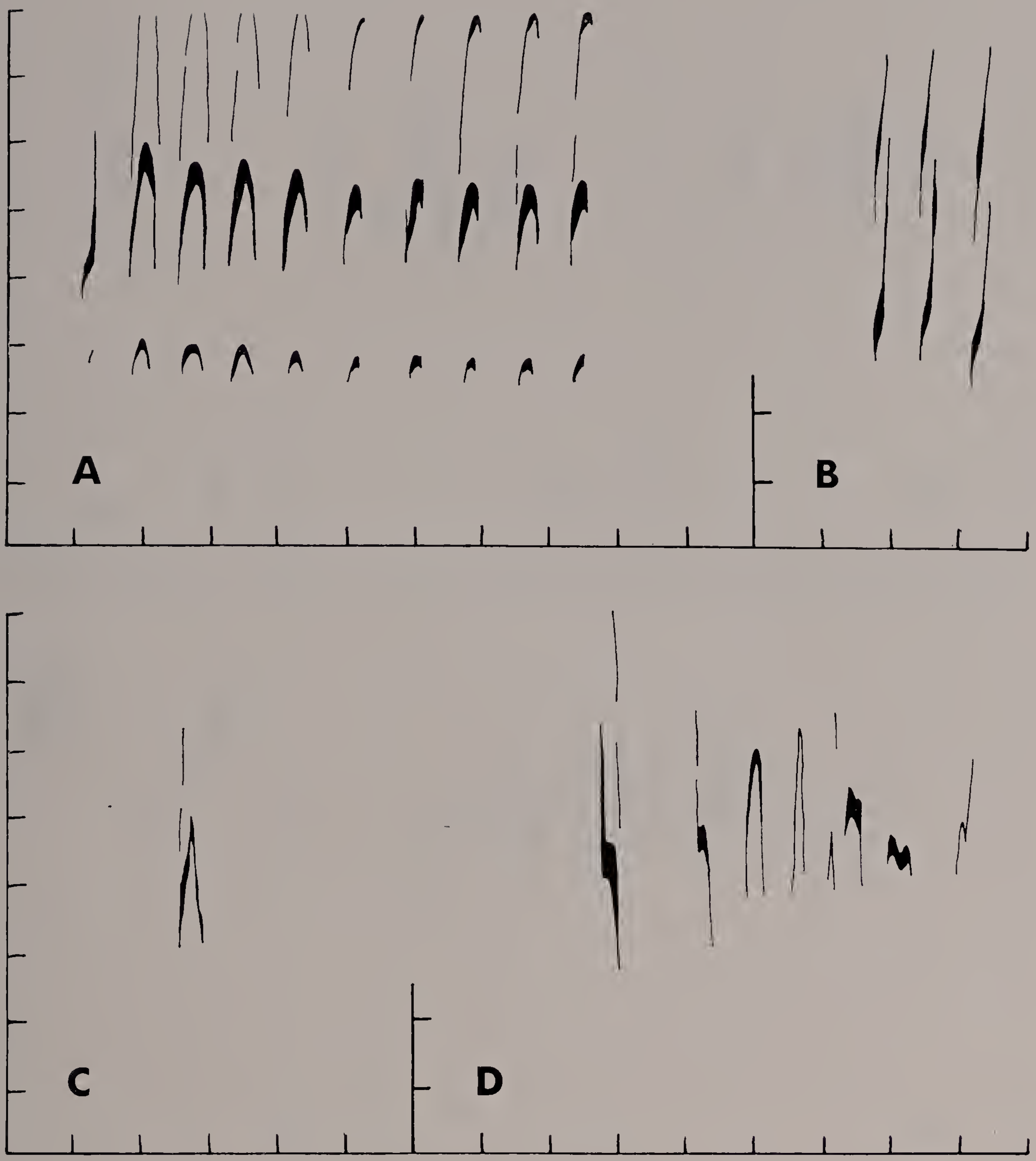
FIGURE 6:3a. Call, probably ILHV, of a lone juvenile (Amapa, Brazil).
6:3b. RV, guarding male (São Paulo, Brazil).
6:3c. Unusual RV, in post-RRV period (Argentina).
6:3d. Late evening RV (Argentina).



Tyrannus melancholicus

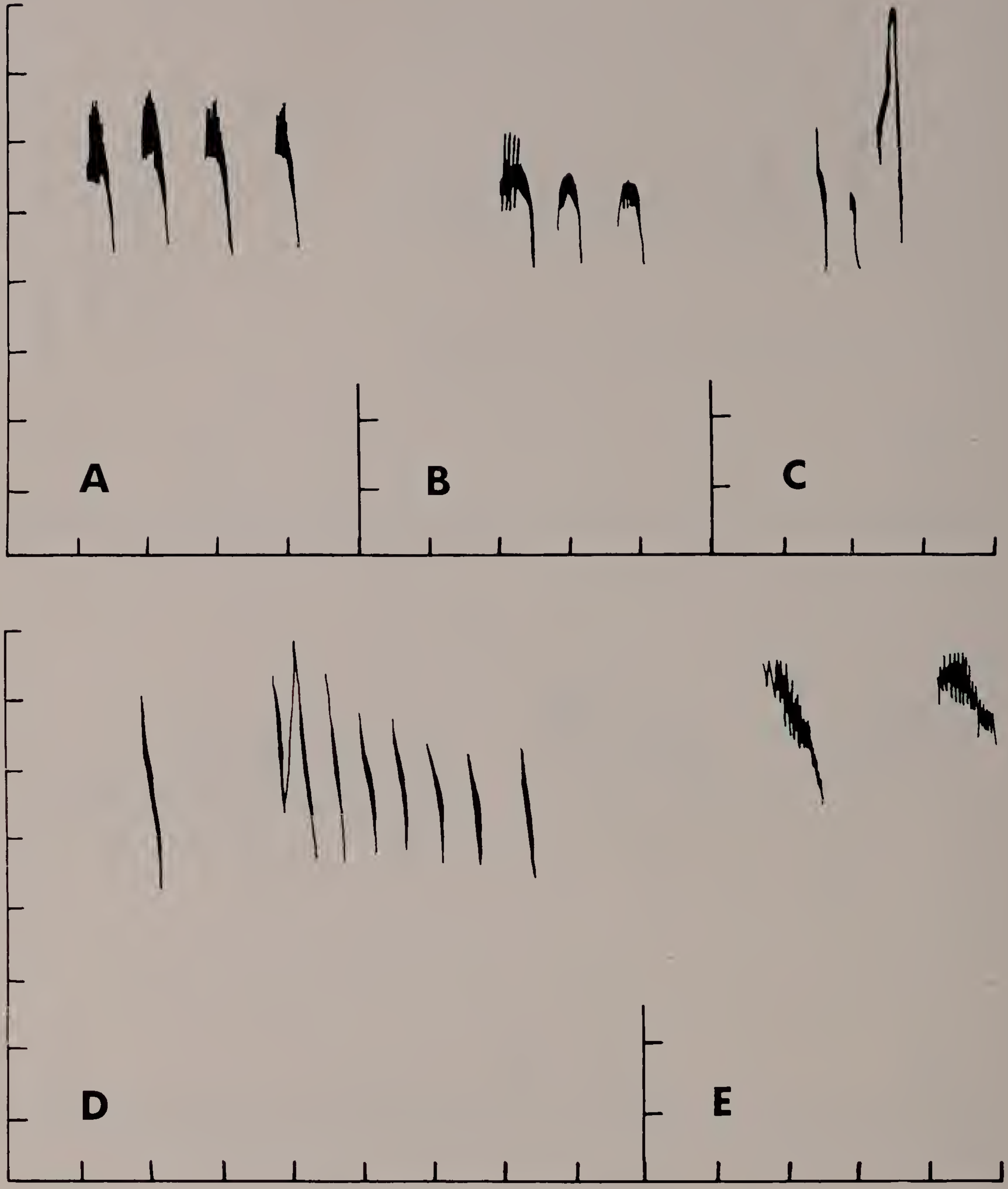
FIGURE 6:4a. Part of a rather slow CV by a female in the nest after the pair had just chased away an intruding Piratic Flycatcher (*Legatus leucophaius*) — Panama.

6:4b. An RRV with a single first phrase, of four elements, preceded by a single element (one other similar element 0.8 seconds earlier was omitted from the figure), and a third phrase of eight elements (Panama).



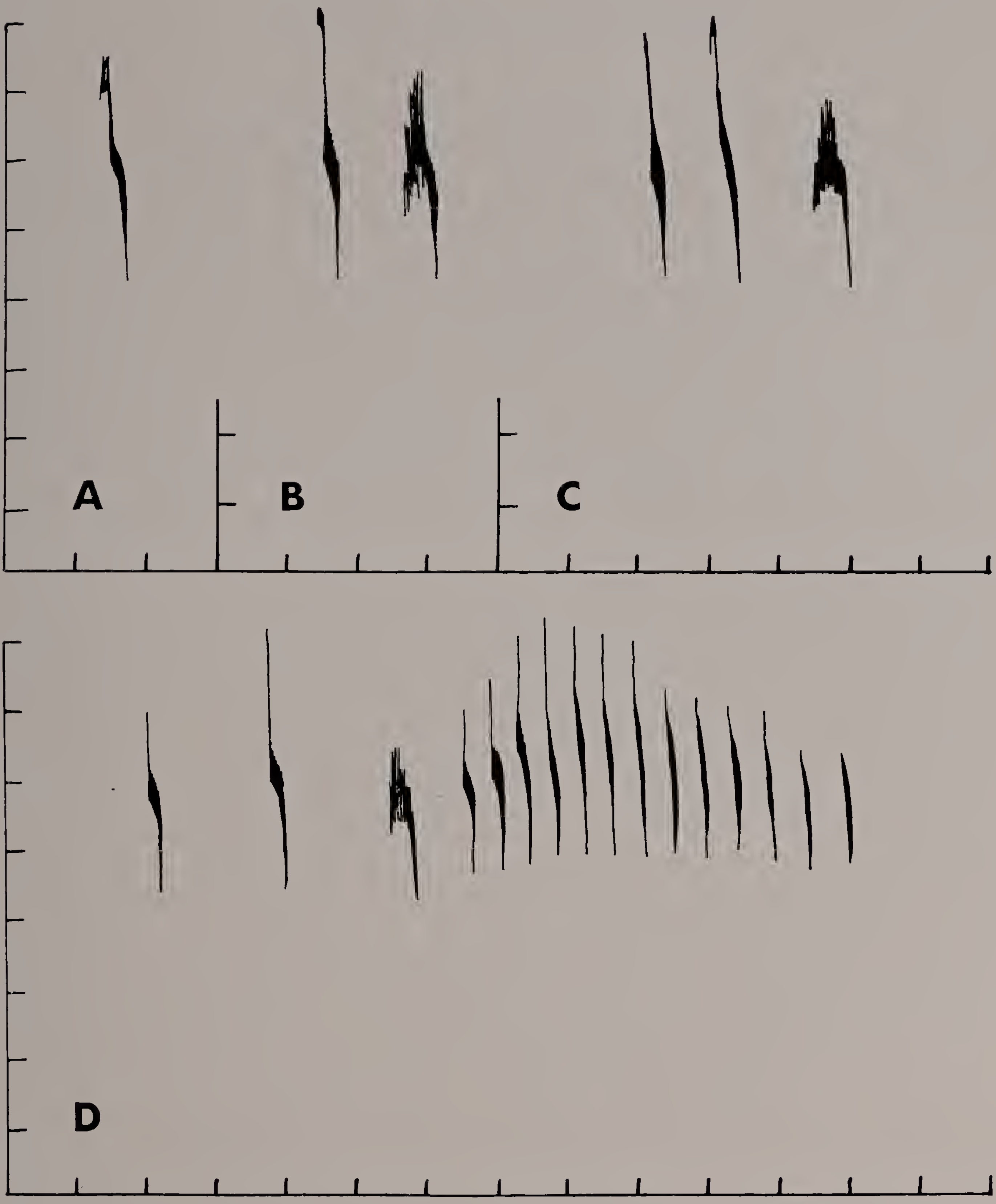
Tyrannus niveigularis

FIGURE 6:5a. LHV of a presumed male, uttered in a greeting between mates.
6:5b. LHV of a presumed female in the same greeting; the second element of this call overlapped with the first of that shown in 6:5a.
6:5c. Brief vocalization of an individual perched alone — probably RV or ILHV.
6:5d. Vocalization used in flight display; probably very like RRV.



Tyrannus albogularis

FIGURE 6:6a. The longer LHV form, uttered in a greeting.
6:6b. The shorter LHV form, uttered in a greeting.
6:6c. A variant of the shorter LHV with a high pitched terminal element.
6:6d. A "tch tchreeeee" from an adult just after returning from a fly-catching flight. This may be an ILHV preceded by an RV. Not all probable ILHVs are associated with RVs, and some are slightly briefer than this one and apparently without connection between their first two elements.
6:6e. Two "tchee" calls (not consecutive) from a begging fledgling.



Tyrannus albogularis

FIGURE 6:7a, b, c. Probable RV: examples of one, two, and three element forms, respectively. Showing only some of the variations. From the calls of the agitated adult of 17 January.

6:7d. Prolonged ILHV form with RV-type introductory units; may be CdV. From the same adult in the same sequence of behavior.

Chapter 7.

WEST INDIAN SPECIES

Tyrannus dominicensis, Gray Kingbird

The Gray Kingbird is a relatively large kingbird, dark gray above and white below (faintly grayish on the chest), with a black mask extending through the eye from the bill onto the ear coverts. The concealed crown patch is yellow or slightly orange. It has a relatively heavy bill, varying somewhat from population to population. It breeds throughout the West Indies and other Caribbean islands, the Bahamas, Florida keys, up both coasts of Florida and the east coast of the United States to South Carolina, and in parts of northeastern South America. The northern populations down to and including Jamaica (but not Hispaniola and eastward) are migratory, and are presumed by Bond (1950) to be at least some of the birds that winter in northern South America.

My observations were made solely in Jamaica, from 3 to 28 April, 1963, with the exception of a few incidental observations made in coastal British Guiana in early March of the same year. I was not able to sample more than a portion of the life history of the species. The birds in British Guiana seemed to be in the early stages of pair bonding, and may have been a mixture of pre-migratory and resident individuals (if, indeed, any do breed there). The first arrivals had preceded me to Jamaica by only a week, and individuals were still arriving when I began my studies. Local individuals had been active in staking out loosely defined territories and in forming pair bonds, and had in the case of two pairs, begun to build nests by the time I left. At least one male was observed guarding near the nest while his mate collected material and built. Despite much countercalling and fairly frequent inter-male or inter-pair squabbling, it did not appear that territories had become rigidly defined, and conspecifics often flew over, unmolested, within sight of a male while I watched, or two to three pairs would feed on fruit in the crown of the same royal palm with rather little fighting. Up to three pairs at a time would visit a small artificial pond in one of my study areas, the Hope Botanical Gardens near Kingston, which had an unusually high population density. To some extent such behavior was limited to certain times of day, and males were not particularly permissive of intruders around sunrise.

I was fortunate to have one consistently recognizable individual which, by its behavior and by the emarginations visible on its primaries when it stretched a wing, could be identified as a male. This bird had lost all of its tail feathers a few days after arriving.

Locomotory Hesitance Complex of Vocalizations

The general forms of the LHV are very similar to those of *T. melancholicus,* although the calls of the two species are easily distinguished, even by human ears. Males typically utter a prolonged, usually slightly harsh introductory element followed by a string of brief, CV-like elements (see fig. 7: 1a). The length of this series varies considerably, but in a simple meeting of the pair, members may be about eight elements long, or, if the birds are excited, up to 35 or more. Long series are likely to be followed by bursts of shorter series (each with an initial prolonged element) which may have only three to five brief elements. Such short calls (fig. 7: 2a) are indistinguishable from vocalizations used in a variety of situations typical of the ILHV in *T. tyrannus,* so *T. dominicensis* appears to have both ILHV and LHV, the former being simply an abbreviated version of the latter.

The response of a female to an LHV by her mate is not an identical call, but, again as in *T. melancholicus,* is a short burst of about four or five elements of which the first is at most only slightly more prolonged and harsh than its very brief successors (fig. 7: 1b). When mates approach closely and are agonistically excited, the female's call may be extended (fig. 7: 1c) to 20 or more elements. It seems in all cases to be at a lower frequency than her mate's, and sounds less shrill. I am by no means certain that each form of the LHV is limited to one sex, but each has appeared to be within the scope of my field experience with this species.

In at least the LHV used by males, the elements following the initial prolonged one are sometimes slightly prolonged themselves, and become harsh sounding (see fig. 7: 2b). This variation apparently correlates with increased aggression in the caller, and the one example of a good aerial fight between two apparent males that I recorded included one series of seven fairly prolonged, harsh elements which may be a strongly aggressive variant of the LHV (fig. 7:2c). In the absence of a more complete set of intermediates, this interpretation must be regarded as tentative; one alternative is that the LHV can intergrade continuously with series of a vocalization which has a message of aggression, and that the latter is a relatively prolonged harsh unit, as in some forms of the RV of *T. tyrannus.* In other intraspecific fights I have occasionally heard (but not recorded) either RVs or calls which suggested that the ultimate elements of the RV can be made harsh.

Whether or not this species has an Attackee Vocalization is also unclear. At least once I have heard single high, thin "tee" calls from a bird in an aerial fight, but I have no recordings. Recordings on hand do include numerous examples of LHVs or of ILHVs in which the initial prolonged element wavers quite markedly and attains up to three peaks. The situations in which such recordings were made suggest intense conflict of agonistic and other drives and bring to mind cases in which western and Mexican species used similar variants.

Repeated Vocalization

The call that gives *T. dominicensis* its Jamaican colloquial name of "petcherry" is probably its RV. The vocalization has two loud, specialized elements, of which the second is considerably more prolonged than the first, followed by about three to five very brief, abruptly ascending elements (fig. 7:2d). It is extremely similar to the CdV but differs in several features: (a) the most prolonged element of the RV is preceded by only one other element, and that is less brief than the corresponding element in a CdV; (b) the second element is usually constant in form, with a gradual increase in frequency; and (c) the ultimate very brief elements usually have their maximum energy in their lower frequencies, and lesser energies as they ascend (as in the ultimate portion of an RRV phrase) rather than the reverse or a relatively even distribution of energy.

The uses of this vocalization suggest strongly that it corresponds to the RV of *T. tyrannus*. It is one of the calls used in countercalling during the daylight hours, it is used by contending males with WFk and Crouching when one is intruding into another's area, it occurs in fights, and it is given by some individuals (probably males) as they settle to roost in the late evening twilight. Females also use it during agonistic encounters. Unfortunately, I left Jamaica just as the first nests were being built and male guarding behavior was just beginning; hence I do not know if the vocalization is prominent during guarding, although it was occasionally uttered by males who were probably guarding. It is sometimes used in patrolling, but much less commonly than is the CdV.

During encounters between two apparent males the RV was used repeatedly by both, and its terminal string of brief elements was reduced to three (very rarely to two) very emphatic ones; this was noted in both Jamaica and British Guiana. Occasionally, when one individual makes a short pursuit of the other, a significantly different variation may occur — apparently usually uttered by the pursuer. In this form the second or prolonged element is replaced by a couple of very brief ones, so that no prolonged elements occur and the whole is somewhat like a condensed version of the brief female LHV. This staccato burst has a very different sound, a "whirr" reminiscent of a Wing Whirr display (which display, interestingly, is known from pursuing individuals in other kingbird species).

Chatter Vocalization

A CV, comprising a series of brief units of ascending frequency, is used by both sexes (fig. 7:3a). The units appear always to have some frequency fluctuation, and may have much; they may be arranged singly or in couplets, but always seem to be more widely spaced than the brief elements in an LHV. I have recorded the display from a nest-building female, and at least once from a female at her nest site using the display instead of an LHV in a greeting with her mate as he landed on a guard perch two feet away. One male gave what apparently was a nest-site-showing display, in which he led his mate to the base of a palm frond, squatted there, and repeated CV series while she watched.

Compound Vocalization

The *T. dominicensis* CdV is used primarily or solely by males, and has two, three, or occasionally more, simple CV units preceding a prolonged element, which is in turn followed by a brief burst of usually five or six simple elements. Sometimes single CV units are scattered at intervals between the longer, more complete calls, as in *T. tyrannus.* There is a great deal of variation (fig. 7:3b, c). The prolonged element, for instance, may be relatively flat or may waver and peak two or three times, it may also break down and be replaced by shorter elements, or it may repeat and be present twice in succession. On the whole, the CdV is somewhat like a very simplified RRV. It is also like the RV with which it sometimes intergrades, and the relative differences have been itemized previously. Its terminal portion is usually more like an ILHV than an RV, and it might be better thought of as a variable vocalization covering the CV+ILHV and CV+RV spectrum. Its usage is very like the CdV of *T. Tyrannus,* and it should be remembered that in that species some variations of the RV portion are intermediate to ILHV forms. Usage includes patrolling, in which it is the most common vocalization, calling while foraging alone (which is probably a combination of foraging and patrolling), and countercalling with other individuals who are using either similar calls or even RRVs. It occurs, but is much less common than the RV, in aggressive encounters and in birds settling down to roost.

Regularly Repeated Vocalization

Description. The RRV of the Jamaican population of *T. dominicensis* is not broken into two phrases, but it sounds almost as if it were — it does, in fact, have two quite distinctive parts as a result of a prolonged and emphasized element, about the fourth or fifth element from the start (fig. 7:4a). This emphasis makes the first part of the call sound more prominent than do the corresponding calls of other kingbirds that have introductory phrases, but the call is easily recognizable as belonging to a member of the genus; in fact, it is very closely similar to the final phrase of *T. melancholicus.* The various elements of the RRV are homologous with units in the RRVs of other species, as will be discussed in a later section. Individuals appear to differ consistently in the form of RRV used by each, and some individuals are recognizable to human ears; almost any of the elements of the call may differ among individuals.

Any one individual may give occasional variations of his form of the RRV, particularly when calling either unusually rapidly, or unusually slowly. Slow calling is typical of the end of a morning RRV session, and most variations at this time tend to be simplifications, making the call more and more like the CdV. Variations at other times are usually of the same sort, but occasionally take the form of a doubling of one or more of the shorter elements in the RRV, making the whole slightly longer.

Use. I began work on this species in Jamaica on 3 April, 1963. The first returning migrants had been seen in the area during the last week of March by I. Goodbody. The Gray Kingbirds began repeating the RRV shortly before 0500 (standard time, as elsewhere in this paper), perhaps delayed somewhat by heavily overcast skies and incipient rain, but fully ten minutes in advance of the next species to sing (*Mimus polyglottos*). At least three birds countercalled vigorously, then ceased for several minutes during the height of the rain, then began again. Calling fell off only slightly at about 0600 and, to my surprise, was still quite considerable by 0900. Indeed, RRV calling continued off and on through the day, and was marked just before a late afternoon rain. At about 1800 there was more RRV after the rain, and the last use of it was at nearly 1900. For the next several days, RRV in countercalling by several birds at a time was common throughout the day, particularly during times of overcast skies. By 7 April most males would not call the RRV after sunrise with any regularity, if at all, but other individuals still continued late into the morning. By 9 April, most individuals had stopped calling by 0530 (one began again briefly at 0810 when a cloud passed over the sun) but a very few lingered on; the incidence of calling by all males had waned considerably in the past two days. On 11 April, for the first time, I heard no individuals call during several hours after the predawn chorus.

At least two changes had taken place between late March and 11 April. First, there had been considerable rain and overcast skies until 9 April, and the incidence of RRV calling was always highest at (although calling was not restricted to) times of low or obviously changing light intensity. Second, most or all of the males I was observing had formed pair bonds by 11 April. Some pairs had begun to form by 5 April and appeared stable by 7 April. In other cases males remained unpaired until as late as 10 April, or, if paired, did not spend enough time with their mates for me to discover the relationship. It was the latter males who used the RRV most after the predawn chorus; males forming pair bonds were usually active with their mates by sunrise and only rarely paused and countercalled with a neighboring male. By the time the pair bonds appeared stable these males were not likely to use the RRV after the predawn chorus even when countercalling. These observations indicate that both the persistent low light intensity of the period up to 9 April and the unpaired status of some males were factors partly responsible for the extended daytime use of this vocal display. Even though the relative influences of these two factors cannot be separated they do point to a greater likelihood of daytime RRV in this than in most other species of kingbird. A further factor, the unusually high population densities on my study areas, also almost certainly contributed to the amount of use of the RRV.

Even as late as 13 April one *T. dominicensis,* who had apparently paired relatively late, used the RRV until after 0700 on a bright, sunny morning. On 19 and 22 April another bird gave a few phrases when heavy clouds piled up briefly in mid-afternoon. Apparently some males are more prone to give the RRV after sunrise than are others, even under the same conditions of overcast skies and paired status. By 22 April, however, the predawn calling itself had dwindled to almost nothing, although it increased slightly thereafter. On 24 and 25 April, the last days on which I listened for it, RRV calling began on one of my sites in the black of night (0415) fully 30 minutes before it began at the other site. It was over by 0510, at which time only a very few other passerine species had begun to "sing," and the kingbirds were then active. That the call should be used in these instances only until it was light enough for the birds to begin moving about, and should be used during the day earlier in the season only until a bird had a mate, suggests that it occurs only when a male is unable to take part in the activities typical of a pair. Whether he calls because frustrated from such activities, or in response to a mood which is superseded once he is paired, is not clear.

Two other instances of post sunrise use of the RRV are of considerable interest. On 14 April, in a region several miles remote from either site, I witnessed in mid-afternoon (1600) a territorial dispute. One bird quickly routed the other and drove it out after a hard chase. A third individual was present and followed the chase; this was likely a female. After winning the encounter, the aggressor perched and gave one complete RRV. The second instance is much more difficult to interpret. On 13 April at the Hope Garden site one bird, apparently paired or becoming paired, continued to give occasional RRV until about 0700. Shortly before 0700 two other *T. dominicensis* flew overhead on two occasions without responding to him or eliciting a response from him. Remarkably, they were also using the RRV — the only case of its use in flight that I have seen. (This may have been intermediate display of some sort — it is fully described under the section on Tumble Flight.)

Use of the RRV apart from in the predawn chorus was often marked by at least minor irregularities. The most extensive irregularities, however, occurred in the unusually early calling (beginning at 0415) on 24 and 25 April. This early calling was started by one individual; most of his neighbors quickly joined in, some remained silent. Most of the birds which did call used simplified forms of the RRV, and these abbreviations resembled CdVs. The most intense caller at times reached unusually high rates of repetition and made frequent "errors," sometimes simplifying his RRV, and sometimes slurring it by doubling shorter units.

Finally, the RRV heard and recorded in British Guiana is sufficiently different in form (fig. 7:4b) from that of the Jamaican birds to merit discussion. In a species such as *T. dominicensis,* in which most of the breeding populations segregate on different islands, there must be considerable barriers to gene flow which are not much (if at all) alleviated by the partial sympatry of wintering groups (synhiemy, Salomonsen, 1955). The more elaborate form recorded in British Guiana is clearly of the general pattern of this species, and not confusable with any known RRV of any other *Tyrannus* species. It looks very much as if the first part was nearly equivalent to the whole of a Jamaican RRV, and the second part was a repetition of the last half of the first (fig. 7:4). If so, its various elements are not really much different from the corresponding elements in the calls of Jamaican birds. Its less emphatic onset and greater length make it more comparable to the whole RRV of *T. melancholicus,* although the matching to the final phrase is less close. Conceivably, it represents but one of several different forms the display might take in different populations. That it should have been used at all in British Guiana, along with such other vocalizations as the CV, suggests that either pair formation may occur on the wintering grounds in late winter in some cases, or that breeding may occur in the vicinity of Georgetown, British Guiana.

Tumble Flight

In observations made over 25 days, from arrival of birds on the breeding grounds until the first nests were built, I did not see this display. On 13 April I did, however, see a performance by two birds that probably contained elements of the Tumble Flight, at least as the display is known in some of the other species of kingbirds. The observation has already been mentioned in the discussion of the RRV. Two kingbirds were twice seen flying over the Hope Gardens at about twice the height of the taller trees; one appeared to be chasing the other, although it was not a "hard" chase — their flight was not exceptionally rapid, there was no twisting or turning, and their wing strokes appeared slightly hesitant. In both cases the pursuer was somewhat above the other when they were first seen. It gradually overtook the leading bird and began to call the RRV. With the complex ending to the ultimate RRV phrase of each set it would come to a slight stall, then make a shallow swoop toward the other individual. By the third such stall and swoop it would reach the other and peck at the center of its back. This would be followed by flying slightly up, and then repeating the sequence call, stall, swoop, peck, rise. By then *both* individuals had a distinctly hesitant wing stroke (i.e., they were fluttering); the attacked bird would now begin to call the RRV at the same time as the aggressor started a new set. It did not attempt to fly faster or to turn about and meet its attacker. In both flights the birds continued in this manner until out of my sight.

Without further information it is impossible to understand this behavior. Quite possibly, a male was chasing an almost evenly matched male from his territory; at least the fact that both individuals used the RRV suggests that both were males. It is most unusual that the RRV should have been given in flight unless this was a dual Tumble Flight display (without tumbles); in at least *T. verticalis, T. couchii,* and *T. forficatus* the RRV is the vocalization of the Tumble Flight. The timing in this instance supports the interpretation that the RRV was being fitted into some representation of a Tumble Flight; the ultimate calls of the RRV came just as the bird stalled and began to pitch forward.

Other Non-vocal Displays

Within a pair the LHV is often accompanied by a WFt display in which the wings are usually held out laterally and fluttered as in other kingbirds. Brief LHVs may have little or no WFt, the least expression of the display apparently being to lift just the wrists out from the body. Usually the tail is spread during WFt, but I have not noticed it quiver. Orientations of birds using the WFt are usually parallel (i.e., not facing), and the pose is semi-upright, the bird leaning slightly forward but not usually Crouching.

The WFt may be given from a Crouch, but the WFk is more usual from this position, even if an LHV is being uttered. This combination of WFk, Crouch and LHV occurs often between members of a pair if they have been agitated by an event such as the intrusion of another conspecific individual, and at least the male has reacted aggressively. Crouch with WFk and Tail Flicking is also directed to an opponent such as a persistent intruder, and may precede attack. During Tail Flicking the tail is fanned at least partially (wholly if the bird is very agitated). One morning I saw one individual use Crouch, WFk and Tail Flicking toward a persistent intruder, and then attack, fight, and chase this three times in about 10 minutes; in each case during the attack, fight, and chase there was RRCP or RCP, by the aggressor only, although I did not see Gaping or hear Bill Snaps or Wing Whirrs; he did call the staccato bursts of RV repeatedly. After the last incident he perched and called many RV or ILHV with an extreme Crown Ruffled. Bill Snapping sometimes occurs in attacks.

TYRANNUS CAUDIFASCIATUS, LOGGERHEAD KINGBIRD

One of the more unusual kingbirds, *T. caudifasciatus* looks rather like *T. tyrannus.* It is white below, and has a black head and tail which is dark with a white tip (in most populations). Its back, however, is paler, and often noticeably brownish. The concealed crown patch is bright yellow. Its head is proportionately large, and the bill, at least in the Jamaican population which I studied, is rather long, but the bill varies from population to population, and in at least the Bahaman birds it closely resembles that of *T. melancholicus* (see Bond, 1943). The species is nonmigratory, and occurs only in some of the Bahamas and northern islands of the West Indies.

I observed it only in Jamaica, from 3 to 28 April, 1963. Most of the birds I saw were somewhat in advance of *T. dominicensis* in their breeding cycle, but there was considerable variation. Of four nests I located, the young from one fledged on 15 April, while another was just in the process of being built on 13 April (it later disappeared); the other two had eggs when found early in the month, and these had hatched by the 27th in the one I continued to visit. Bond (1943) cites nests as late as 12 July on Hispaniola. The highest population density I found occupied all of the suitable available habitat in the Hope Botanical Gardens, but this habitat was so arranged that encounters between neighboring pairs were rare. Lacking much interpair interaction, the birds seemed to be usually unexcited, and displayed little.

Locomotory Hesitance Complex of Vocalization

Males have a distinctive LHV, comprising a brief compound unit which is repeated several times as in *T. tyrannus.* The structure of this unit is also in some ways reminiscent of the "kt-ter-ter" of *T. tyrannus,* in that an introductory element is followed by one to four sharply peaked nearly chevron-shaped elements. The sequence of elements usually has at best only a gradual decrease in pitch, however, and the initial element is fairly simple (see fig. 7:5a). The vocalization is used, with the WFt display, when meeting the mate and, at least sometimes, on landing. On several occasions I recorded it during attacks on conspecifics (apparently neighbors), which fled without much resistance; it then sounded even more screeching than usual, and was recognizably different than usual, when analyzed by sona-graph (fig. 7:5b). I have not, however, heard this species use harsh calls during any of the few attacks I have seen.

Females may give a brief reply to such a vocalization, or call alone while passing a mate, but this calling is variable and unlike the form used by the male. Often it is just a brief burst of one to four simple chevron-shaped elements. There may be two identical or fairly similar units followed by one or two dissimilar ones, or just two similar units, or two dissimilar units, or odd groups of three (fig. 7:6a,b,c). These are the briefest patterned forms and may be more properly ILHV than LHV; their elements are often very like the longer (0.02 sec.) CV unit, and sometimes a burst of four such elements or a very slow series of six may be used. Once I recorded a compact, 20/sec. rate CV burst from a female *T. caudifasciatus* as she flew past her mate on leaving the nest. Quite similar calls, equally compact but containing two or three strongly emphasized elements and terminating in a loud unit not of chevron-shape (almost the inverse), were recorded on three occasions when females interacted with aggressive or guarding males. It is not, on the whole, clear that the female does have an LHV, or at least one that is consistently recognizable as distinct from CV, (the chevron-shaped elements are distinct, when they occur). Most of the short bursts of calls used by females in LHV situations are, however, in one way or another comparable to the calls used by females of *T. dominicensis* and *T. melancholicus.*

Three to four element calls, patterned either like the first calls described as used by females in response to male LHVs (two similar units followed by two others) or patterned of three elements ("tee tk-k," fig. 7:6d) have been recorded during countercalling by males who were perched near their mates. These could be either ILHV or RV equivalents, but I have no further data to aid in their interpretation.

Chatter Vocalization

Females use a CV much like that of other *Tyrannus* species in form and occurrence. Very brief units (about 0.01 sec. in duration, see fig. 7:7a) are repeated at a variable rate, usually about 20/sec. Bursts of CV may be as brief as a second (usually these also have less rapid repetition of units, at least terminally — 10 or fewer per sec.) or extend for several seconds. All I have heard were given by females at nests, with one exception. A male stood on a nest rim shortly after his mate had gone off foraging, peered down at the nestlings, and gave a one second CV of 13 units, beginning at the 20/sec. rate, but spacing the last three units considerably apart. Females also sometimes gave this vocalization when coming to the nest to feed the young (in which case the very first elements might be chevron-shaped and hence related to the LHV), or when settling to incubate or brood. One gave it for over a minute once while settling to incubate in the presence of her guarding mate, and he did not leave until she stopped calling. Usually females who gave the CV were nervous, and were often apparently disturbed by my presence.

Females also at times use what appears to be an intermediate between a short CV burst and an LHV in greeting situations (see under LH Complex).

Compound Vocalization

Male Loggerhead Kingbirds have a vocalization which usually includes a prolonged series of simple, chevron-shaped units which, however, are each of relatively long duration (about 0.02 sec., see fig. 7:7b) compared to CV units, although they are also repeated at about 20/sec. (Females sometimes interject one, two or more such units into pauses in an extended period of CV usage, or may utter one or a few in response to a mate's LHV.) In form these are strongly reminiscent of the chatter units in the CdV calls of *T. tyrannus;* in a long series, for instance, there is a sinusoidal fluctuation in pitch, and where the higher frequencies occur, the repetition rate typically increases by 20 per cent. Such series nearly always include a slurred element; the direction of slurring is usually downward (as in fig. 7:7b) but may be upward — particularly if the element is unusually brief. Most commonly this slurred element appears within the first 0.4 sec., but it may also be in the terminal portion of the series, or, apparently not commonly, at both ends. A slurred element in the terminal portion of a series usually comes just after the peak of one of the sinusoidal fluctuations, is followed by three or four standard units, and is preceded only by the standard units of the series. At the start of a series, however, a slurred element may follow either an ascending set of four standard units or a set comprising one relatively high unit preceding two to four lower standard units sometimes arranged in ascending order, sometimes all of one frequency. If the chatter series is brief, it may lack a slurred element, or have only a brief one. Other variations will be mentioned below.

This vocalization not only resembles a CdV, but is also used in similar circumstances. I have heard it most commonly from males countercalling with other birds using similar calls, either in the immediate post-RRV period, or later in the day; sometimes they appeared to be patrolling. Sometimes it will be used in countercalling by a guarding male, but in the three nests I observed, males customarily guarded within a few feet of the nest (often even while the female was on the nest) but were usually silent.

Some of the variation recorded in early morning countercalling is peculiar to the start of a series and too variable within my sample to permit much generalization. Basically, it seems there may be a simple introductory unit which can vary in frequency and form, followed by about one to four brief, closely spaced units usually all at one frequency and sometimes terminating in a slurred element. This set may be followed by a long or short series of the standard chevron-shaped units, or sometimes by no such series and may be repeated. Possibly it represents the RV of the species, but the birds I watched were so quiet during much of the day, including most situations in which an RV might be expected to occur, that this is really only a guess based upon the association of this particular variation with this apparent CdV equivalent.

Regularly Repeated Vocalization

Tyrannus caudifasciatus has perhaps the briefest and most atypical RRV of any member of the genus. Basically, it comprises two units (fig. 7:8a) which sound like "peerr" and "peer-too" (or sometimes "pee-too" or other slight variations), and the two are usually uttered in sequence. The second, however, is rather variable in sound and certainly in form, pauses between couplets may be of quite unequal duration even at the height of calling, and the "peer" unit may be repeated before the second unit is uttered. The regularity of this vocalization is, in other words, usually noticeably imperfect. Yet there is no doubting that this is the RRV of this species; it is the call which is uttered over and over by males for 20 to 30 minutes in the pre-dawn twilight, from a small number of perches in the area in which they roost on their territory. Males use it in countercalling with one another during this period, or call in the absence of other individuals. They rarely use it at other times of day — in fact, I have heard it only twice in post dawn countercalling, and one version used was an extreme variant, while the other was a contraction of a "peerr" unit (fig. 7:8b).

While the vocalization is relatively very simple for the genus, it appears as if it may be merely a reduction of some form similar to that used by *T. dominicensis;* this speculation will be pursued further later.

Non-vocal Displays

As has been mentioned, a WFt display accompanies the LHV during some meetings of the members of a pair. Birds using the WFt adopt the upright pose of *T. tyrannus,* hold their wings straight out to the sides, flutter them rapidly through a small arc, and adopt a Crown Ruffled. WFk has been seen once, used by a nervous female just before she flew from beside her nest; she did not crouch, but did flick her wings a few times, quickly.

An RCP was seen after one member of a pair, which was driving an Ani (*Crotophaga ani*) from its nest tree, actually grasped and hung to the fleeing Ani's back briefly; when this bird perched, its concealed crown patch was clearly exposed. In another case, as a female settled on her eggs her mate chased another bird, possibly a conspecific, out of the nest tree twice, using Bill Snaps in both pursuits.

Various other displays, including a display flight, were not encountered in this species. As has been mentioned, however, none of the individuals with which I worked was particularly excitable or demonstrative; I am quite satisfied that I have not sampled the whole repertoire.

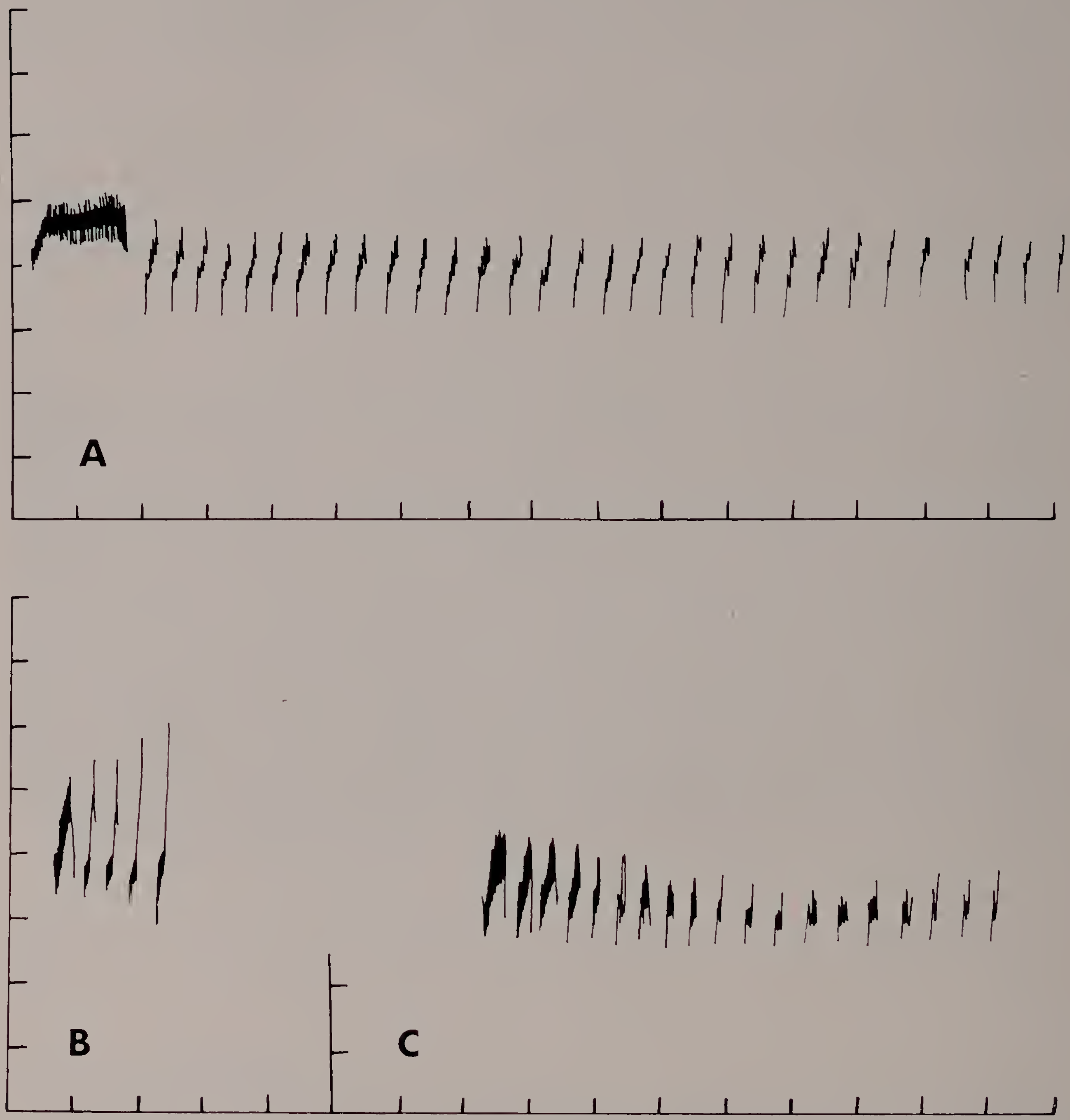
Displays of Nestlings and Fledglings

Both nestlings and fledglings utter a highly variable, wheezy sounding begging call, and certain clearer but also highly variable notes (fig. 7:8c). I was not able to make any ontogenetic studies of the vocalizations.

TYRANNUS CUBENSIS, GIANT KINGBIRD

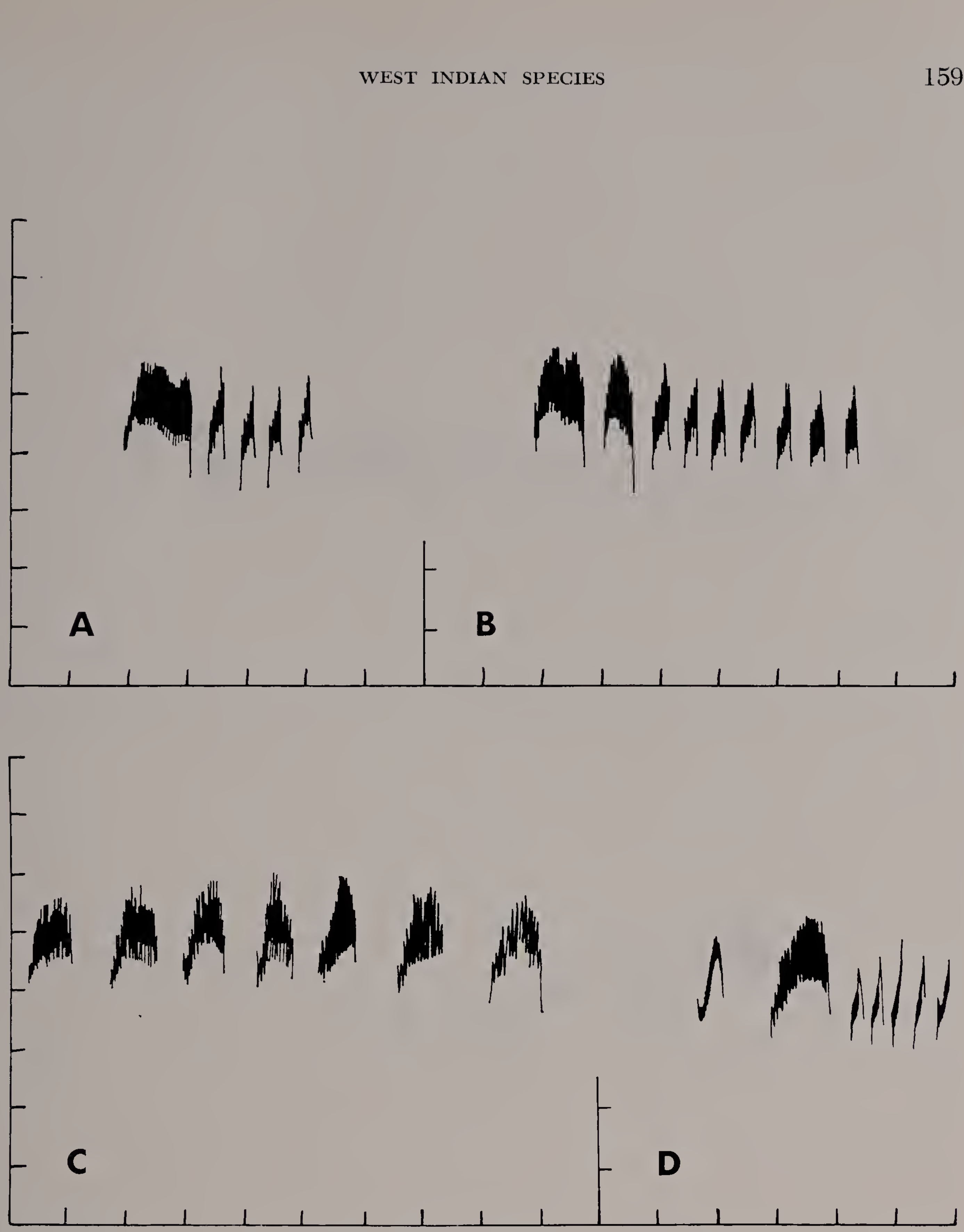
This, the largest of the kingbirds, resembles a Loggerhead Kingbird in the color and pattern of its plumage but is a very large-billed, heavy-headed bird, superficially not unlike a Kiskadee (*Pitangus sulphuratus*). Its range is quite restricted: Cuba, the Isle of Pines, Great Inagua and the Caicos Islands (Bond, 1950). It is the one species of kingbird which I have not seen alive. To my knowledge, no tape recordings of any of its vocalizations exist. James Bond, who is familiar with it and who has an exceptionally fine ear for bird calls, has compared it to *T. tyrannus* and *T. caudifasciatus* (Bond, 1961) and to *T. dominicensis* (pers. comm.). He is apparently not familiar with its RRV, but the calls he has heard from the species during the day have all been what he describes as a “rolling chatter,” that is, series of similar elements.

Figures



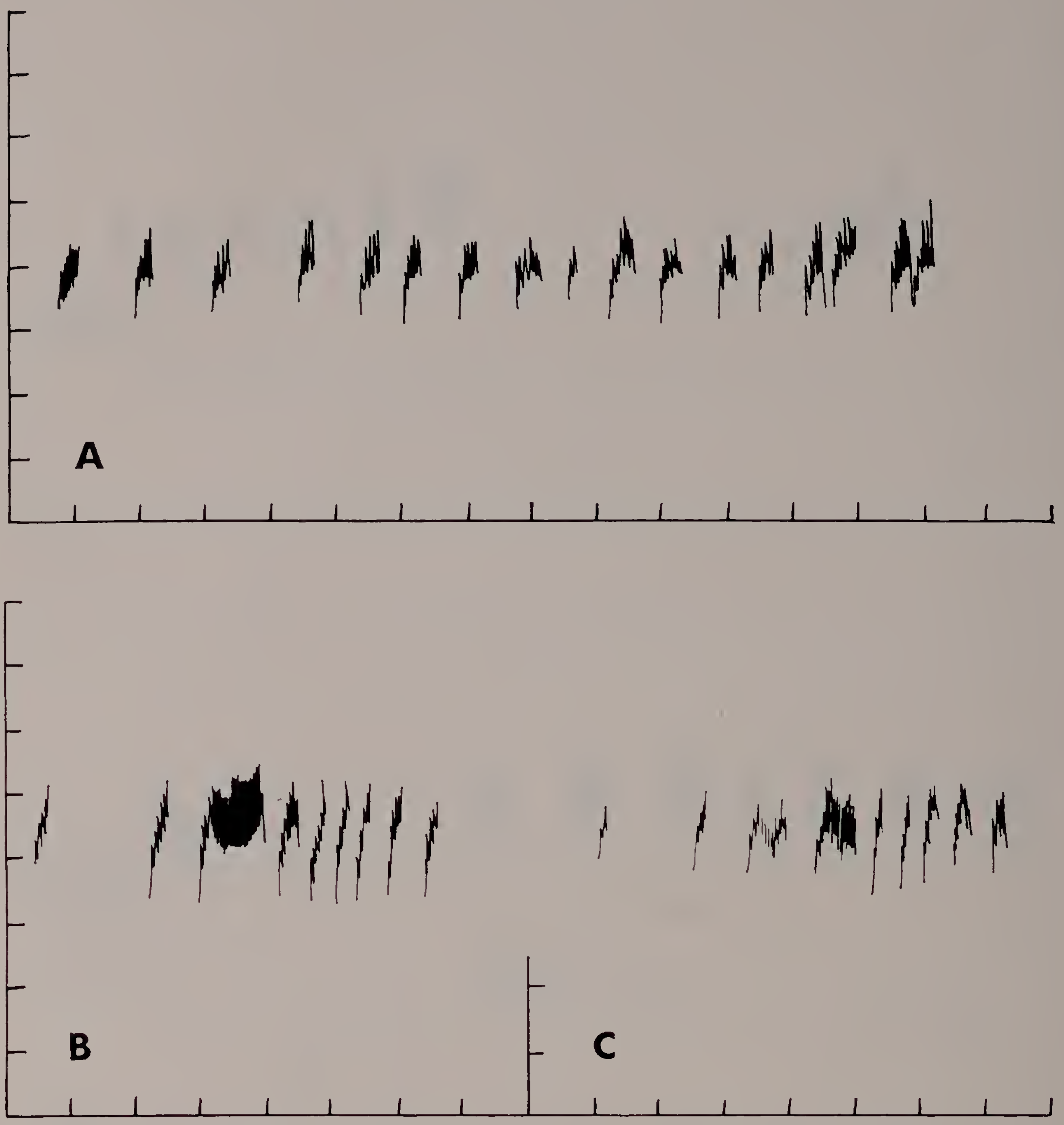
Tyrannus dominicensis

Figure 7:1a. LHV by male in flight, greeting his mate (hers brief, not shown).
7:1b. LHV, brief form usually uttered by females in greetings.
7:1c. LHV, more prolonged form uttered by female, in greeting with her mate.



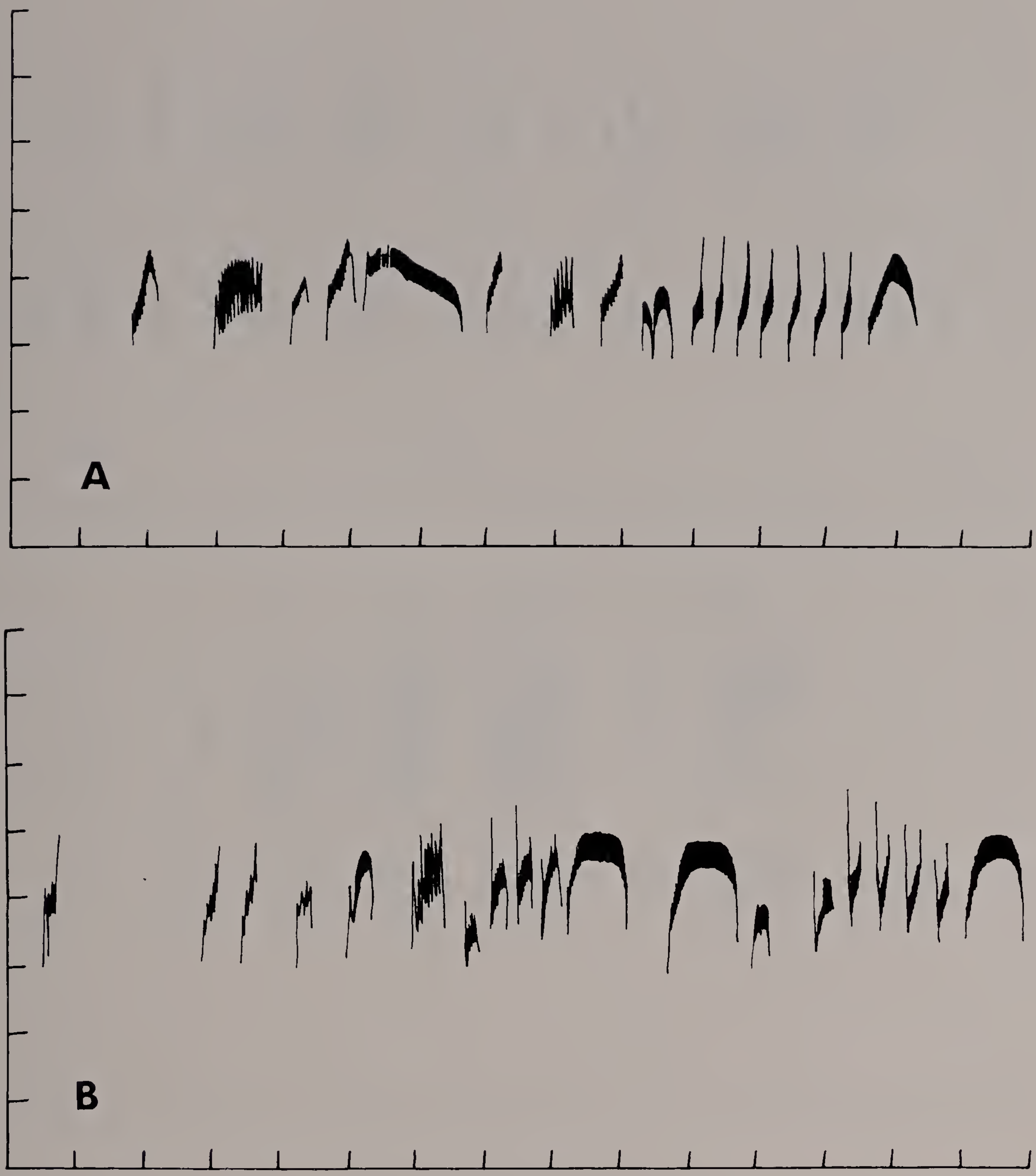
Tyrannus dominicensis

FIGURE 7:2a. Short LHV or ILHV by a male, after uttering a more prolonged form.
7:2b. Harsh LHV of a male.
7:2c. Harsh calls by one individual during an intraspecific fight.
7:2d. RV, during countercalling.



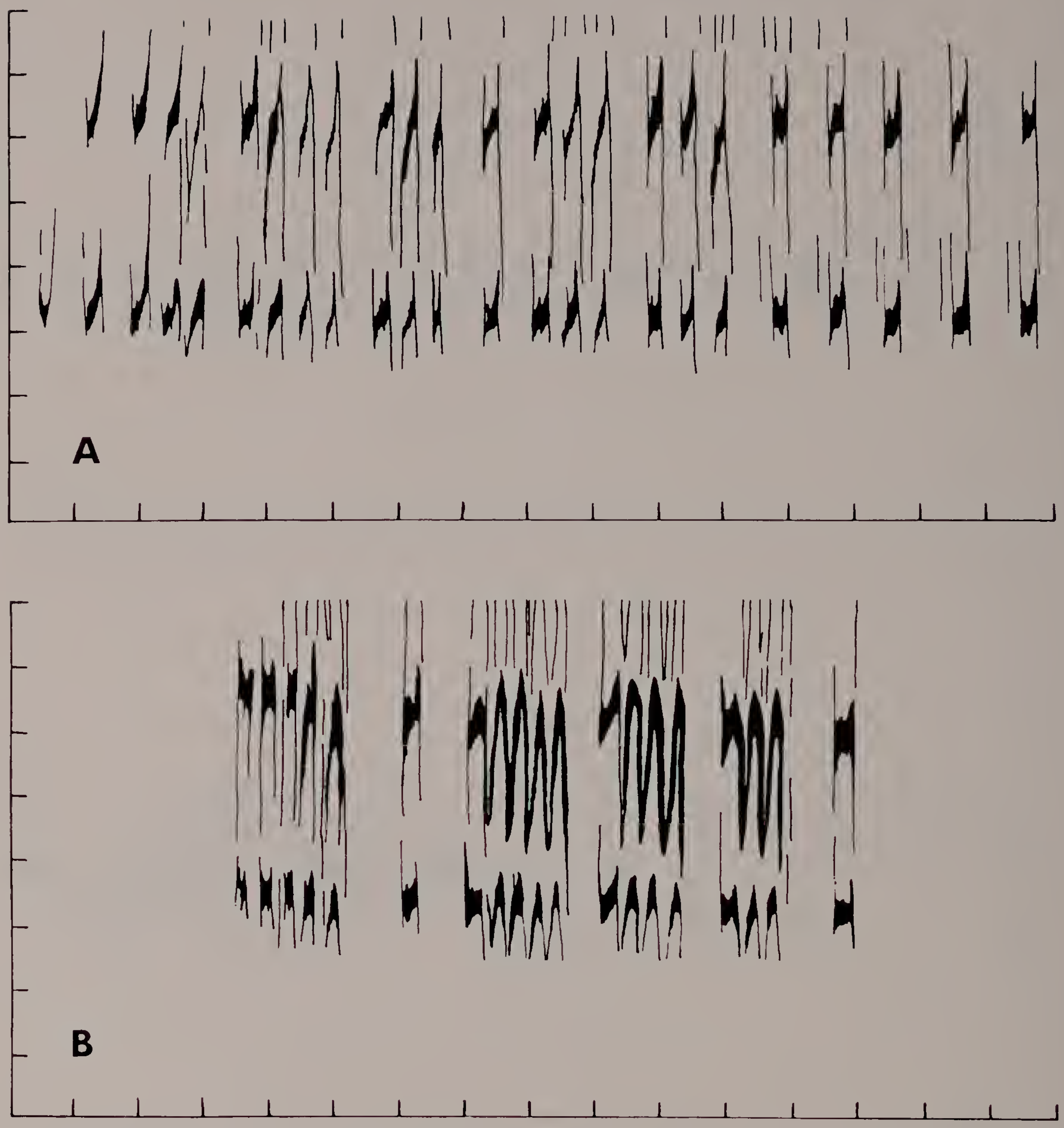
Tyrannus dominicensis

FIGURE 7:3a. Start of a prolonged CV, probably by a nest-site-prospecting female.
7:3b. CdV of a countercalling male.
7:3c. CdV variant of a different countercalling male.



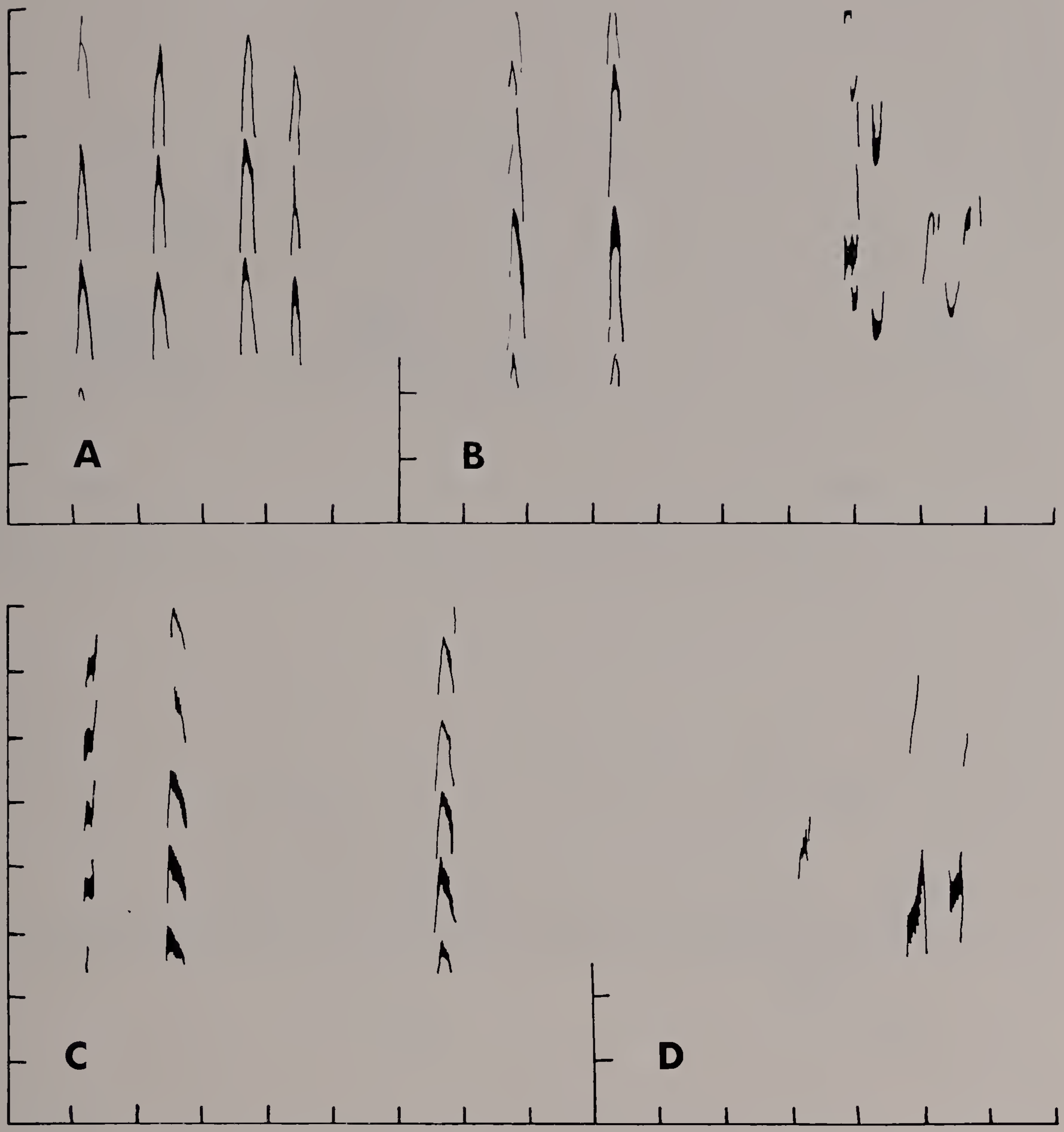
Tyrannus dominicensis

FIGURE 7:4a. RRV, example from a Jamaican individual.
7:4b. RRV, the example recorded in British Guiana.



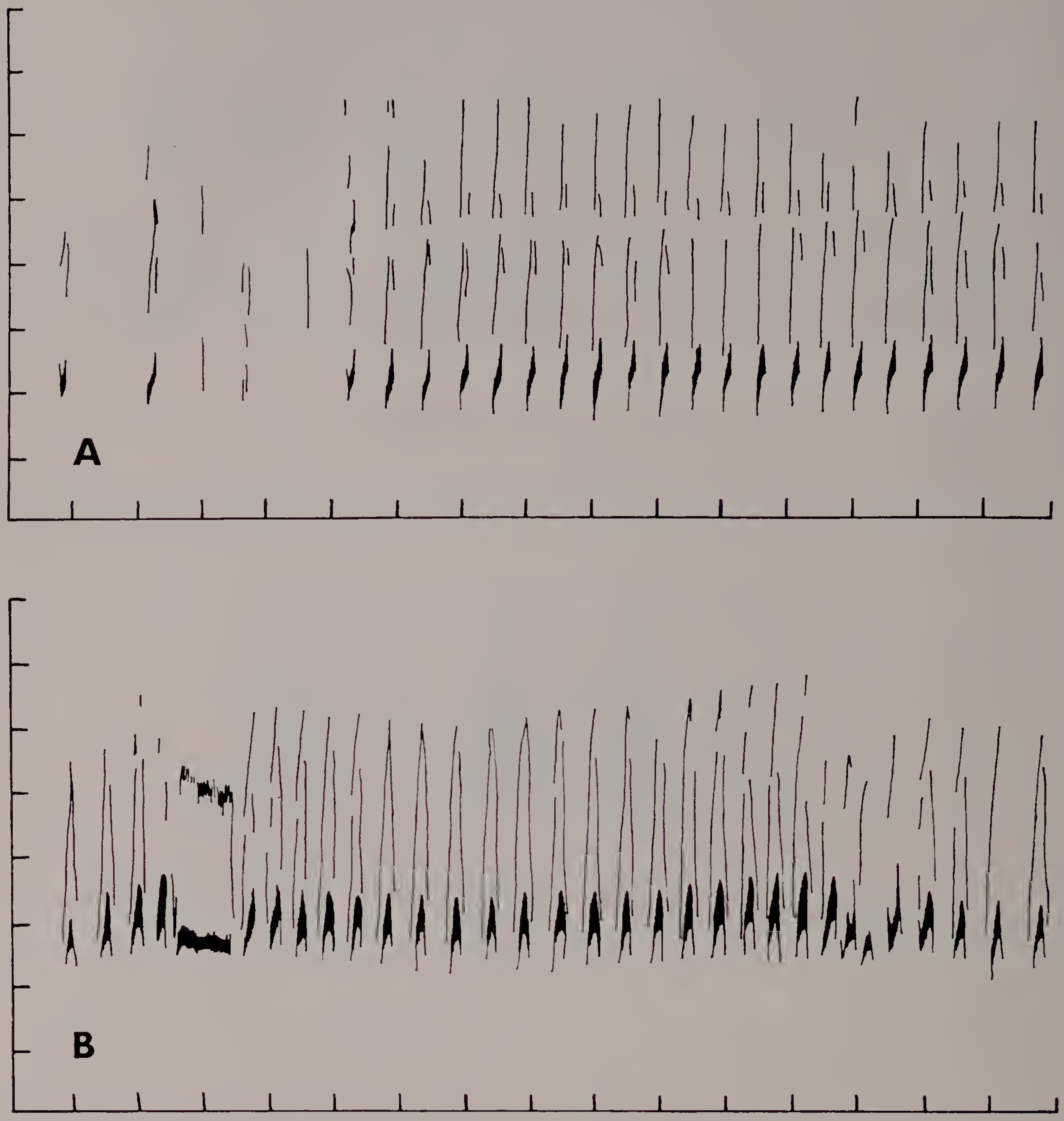
Tyrannus caudifasciatus

FIGURE 7:5a. LHV of male greeting his mate near the nest.
7:5b. LHV by a male shortly after attacking a conspecific intruder.



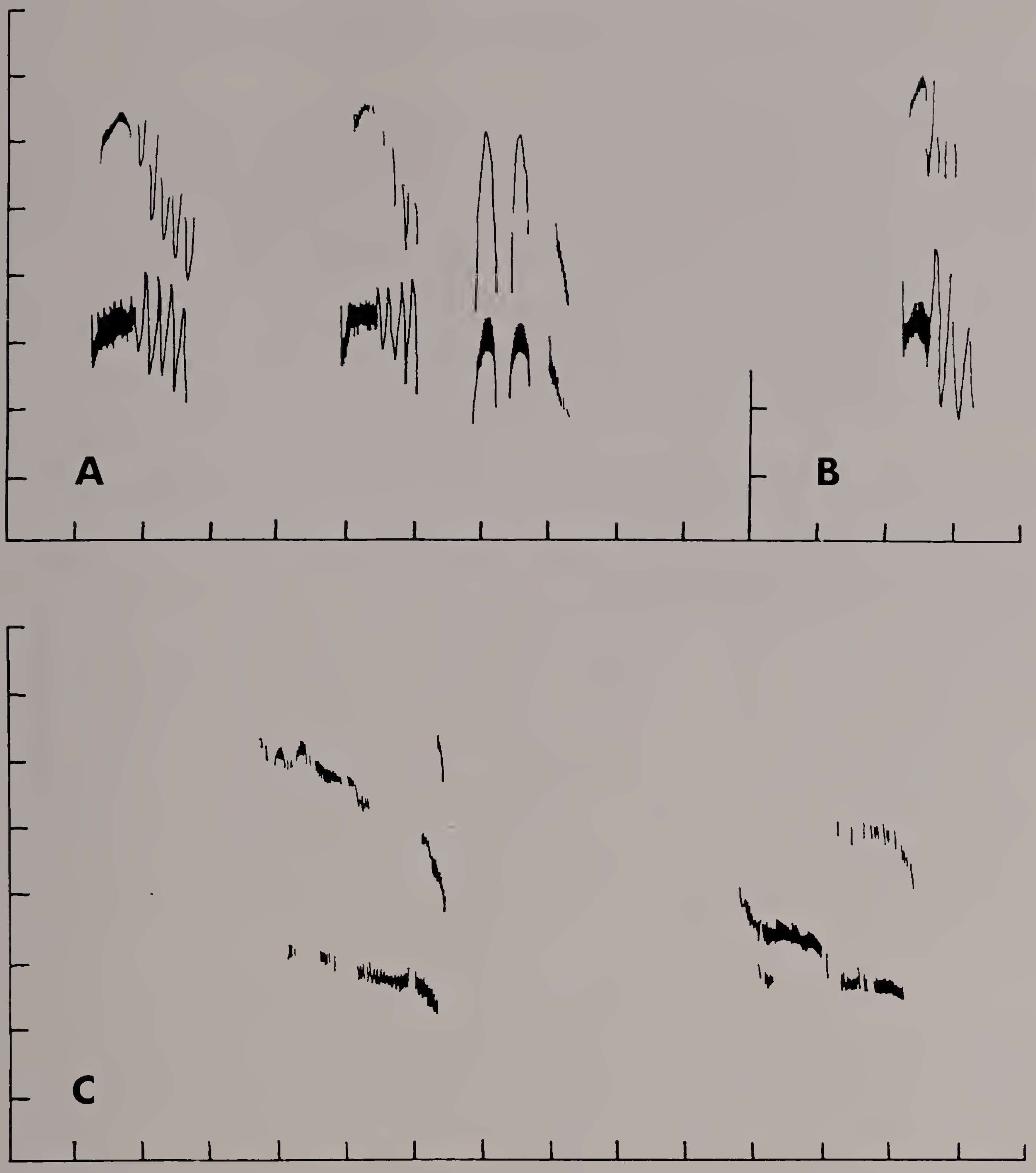
Tyrannus caudifasciatus

FIGURE 7:6a, b, c. Various forms of the call used by females in greetings with their mates.
7:6d. "tee tk-k," probably by a male.



Tyrannus caudifasciatus

FIGURE 7:7a. Beginning of a CV uttered by a female settling on her eggs.
7:7b. CdV of a countercalling male.



Tyrannus caudifasciatus

FIGURE 7:8a. RRV
7:8b. Contraction recorded in post-RRV calling.
7:8c. Two examples (not consecutive) of calls used by begging fledglings.

Chapter 8.

MUSCIVORA, A POSSIBLE SUBGENUS

Two species of kingbirds, the Scissor-tailed and Fork-tailed Flycatchers, which look much alike but which are distinctive within the genus, are small-bodied birds with extremely long, forked tails that stream out behind in flight and are scissored open and shut during the aerial maneuvering at which both species excel. Both are birds of savannahs or savannah-like country and both behave in general much like the other members of the genus. Most of their structural and behavioral characteristics which make them slightly distinct from the subgenus *Tyrannus* may be results of adaptation to their open, nearly treeless (in most cases) habitats.

It is possible, in fact, that these adaptations have been convergent rather than parallel, and that the two species are not closely related within the genus. This possibility will be discussed further in chapter 11, but it cannot be resolved with existing information. Hellmayr, Ridgway, and most recent taxonomists have considered "*Muscivora*" to be a separate genus. While not willing to accord the two species that status, I have chosen to treat them, throughout the book, as if they constituted a subgenus, in spite of the possibility that such a grouping is polyphyletic. This procedure has two advantages: it is relatively conservative taxonomically, and it avoids the awkward wording involved in making all references to the grouping tentative. The grouping leads to interesting behavioral and ecological comparisons whether it is taxonomically correct or not.

TYRANNUS FORFICATUS, SCISSOR-TAILED FLYCATCHER

The Scissor-tail may be considered by most people the most beautiful member of the genus. It is very pale gray below, and only slightly darker gray above; the back is tinged with pinkish or brown. There is a trace of a dusky loral mask, the throat is white, and the concealed crown patch is bright orange-red with slight white edges. The preaxillar feathers are nearly scarlet, and the under wing coverts are salmon pink, which color fades farther out on the lower surface of the wing to a pale pink or white. The under tail coverts are pink, and the bright salmon pink color is repeated on the three outer rectrices, the terminal parts of which are nearly black like the other tail feathers and like the remiges. The adult female can easily be distinguished on sight from the adult male (the only case in the genus) — all of the pink areas are paler in her plumage, and her outermost rectrices are much less elongated.

The species has a restricted breeding range, including suitable habitat in Texas and in the neighboring parts of adjacent states, and northern Mexico in the states of Nuevo Leon and Tamaulipas. It is migratory, and winters from southern Mexico south to the subarid parts of western Panama; a small number of birds also winters in southern Florida.

I observed this species on the Edwards Plateau near Austin, Texas, from 26 through 28 May, 1962, at a time when local females were incubating. In 1964, my wife and I made a set of observations from 20 to 22 May at Laguna Atascosa National Wildlife Refuge in the lower Rio Grande delta, when nest building was just beginning. A very useful life history study has been done by Fitch (1950). This shows that with respect to territorial defense, the mobbing of predators, nest building by the female, and other behavior, the species is typical of the genus. One interesting discovery of Fitch's was that, even during the nesting season, males gathered to roost communally at night (along with some apparently unmated females). This seemed to be the case in the population I observed in 1962, or, at any rate, males could be seen in the late evening dusk flying to the trees of a small arroyo. As far as we could determine in the limited time available in 1964, however, males did not roost communally. The site at Laguna Atascosa was much more heavily wooded than the Austin site, suggesting that males may roost communally only where there is a relative shortage of good roosting trees. Whether or not this is the case can only be demonstrated by more intensive field work. Outside the breeding season the species apparently forms large flocks, and communal roosting is the rule.

Locomotory Hesitance Complex of Vocalizations

The LHV of males is rather variable, but is based on an initial loud, descending element followed by a series of extremely brief elements The latter are usually quite faint beginning shortly or immediately after the initial element, but often become quite loud subsequently. There may be none or very few of the brief elements, or there may be a long series; particularly after a longer series there is usually a harsh burst (see fig. 8:1a). The initial loud element may be preceded by a similar harsh burst, or by an RV, or by nothing at all. The whole LHV may be repeated immediately, but usually not more than once. In general, the shortest forms may be used more often by active birds and the longer forms by unmoving individuals, but this is not yet certain.

The LHV of females is also rather variable, but is simpler and shorter. The basic unit is harsh, with or without an initial RV-like prefix, and may have a very brief harsh burst as a suffix (fig. 8:2a). Some form is discernible (not by human ear, however) within the harshness; there may be from one to three peaks, and there may be a general tendency for the frequency to slope upward, downward, or to remain level. Variability is enough to make my sample too small to show whether or not any of these variations correlate with particular activities, especially since in many cases the slope of the vocalization is obscured by the pervading harshness (seen in sonagrams as a dense cluster of nearly vertical lines).

Individuals of both sexes use the LHV in greetings. Typically a male utters one or two calls, and his mate one or two, although she may utter up to about six and he may add another one or two after a pause following his first two calls. Both birds use the WFt with the calls in most or all greetings, and adopt the not-facing orientation typical of other species. In two copulations or attempted copulations which we witnessed in 1964 (both when the female was on the nest) the male gave an LHV just prior to mounting, both individuals were silent for just over a second after he mounted, and then one (the female?) began a long string of flat, closely spaced LHV units and apparently struggled until the male dismounted and flew off; once he gave an LHV as he flew from her back, the other time he gave a brief burst of harsh CV.

Scissor-tailed Flycatchers of either sex may use the LHV and WFt when landing near or on the nest, even in the absence of the other individual. This is particularly likely if they are agonistically aroused, and the pair which was persistently disturbed by House Sparrows (*Passer domesticus*) in 1964 often showed signs of apparent uneasiness. The male of this pair was watched as he guarded in the early morning; during long absences of his mate he would gradually become more and more agitated, shift and pivot on his perch, and make flights to and from the immediate region of the nest. He often used one or two LHVs as he landed by the nest, flew from it, hovered beside it, or as he returned to a guard perch. Similarly, his mate, when she was hovering beside the nest apparently uncertain as to whether or not to approach it or to leave it, often repeated her LHV.

In the early morning situation just mentioned, when the male was alone on guard near the nest and was becoming agitated, he would sometimes call the LHV without flying. In fact, if he gave two reasonably long LHVs in quick succession he was unlikely to fly or shift on his perch. Often, however, he did give a WFt with these calls, indicating perhaps some locomotory hesitancy. Occasionally, though, he did not use the WFt. One morning there was a period after his RRV calling in which he used occasional LHVs, without WFt and without movement. This also occurred one morning in 1962 in the post-RRV period, when the male I was observing used occasional LHVs (e.g., fig. 8:1b) usually without flying and without WFt, while countercalling with two other males who were behaving similarly. In all of these cases, including the guarding, the post-RRV calling and the post-RRV countercalling, there was an almost continuous use of the RV (sometimes combined with brief harsh units, see CV) by all of the males concerned. The LHVs came amid these other calls, and the effect was quite different from the use of an LHV in a greeting. The RV strings and the LHVs were combined to form what might be called a Compound Vocalization, but I am not convinced that in this species the combination is actually ritualized. Further, the not infrequent use of the same LHV in hesitant flights during the calling or when the bird moved on its perch, and the use of WFt in many instances lead me to suspect that there may have been some locomotory hesitance in the motivation of all of the birds in each case when the LHV was employed. It would be difficult to prove or disprove this, even with an extremely extensive set of observations. It was characteristic of these situations, however, that if the bird was not vocalizing extensively, the calls were almost exclusively RV and he would move little, appearing to be not much agitated.

Repeated Vocalization

The RV is a simple, chevron shaped call, varying slightly in frequency. It also varies in form, tending in many instances to become asymmetrical, such that all of the sound energy becomes concentrated in the arm of descending frequency (fig. 8:2b, c). These variations intergrade with CV (q.v.). Occasional doubling of the RV, forming couplets, apparently relates to the RRV (q.v.).

Males use the RV commonly in post-RRV calling, countercalling, patrolling, and guarding. When the male we watched in 1964 would become increasingly agitated and begin to make frequent visits to the nest while his mate was absent, he would shift gradually from the symmetrical form to the asymmetrical form, and often begin to intersperse brief harsh calls among the RVs. This is apparently typical of birds that appear to be anxious. For instance, his mate sometimes used the RV when visiting the nest (particularly in his absence) and if she did not appear to be very disturbed would use the symmetrical form (when apparently completely at ease she did not call at all). If, however, she acted upset, approached the nest and stopped short, or hovered by it for some seconds, or if she was pestered by a House Sparrow while she was in or near the nest, she would use instead either the asymmetrical form or the CV. Either sex used the symmetrical form (sometimes along with LHVs) while attacking a House Sparrow, but used the asymmetrical form if it took notice of one of the smaller birds but didn't attack.

Chatter Vocalization Complex

The CVs I have recorded from Scissor-tailed Flycatchers mostly conform to a pattern, but the pattern seems to be different in some respects from anything known in the other kingbirds. The simplest form of CV a female has used in working on her nest while I was recording appears to be an RV in which the two arms have been separated by a brief, silent, gap (fig. 8:2e). This intergrades with the asymmetrical form of the RV, in which there is no first arm, or, if present, there is no gap, and the first arm is vertical and faint. In the CV, however, the first arm is likely to be separated even farther than in the simplest form, to be relatively faint, and sometimes to be harsh (fig. 8:2f). Often this ascending first arm leads into a zone of harshness which bridges the gap to the second, descending arm, and the zone of harshness may have discernible within it the form of the female LHV. In fact, the form of the female LHV may be the first part of a CV unit, even when there are several elements to the LHV (fig. 8:2g). In short, the CVs recorded from females appear to provide a complete set of intermediate forms between the RV and the female LHV. All of the CVs have been relatively faint in my experience, and all have been used in or near the nest. Their usage corresponds nicely with their apparent position in the continuum; those most like RVs are given by females when they appear only slightly disturbed; those most like LHVs are used during and after greetings with the guarding mate, as the female settles into the nest. As the 1964 female settled into her nest after using the LHV type of CV, she would gradually modify it into either brief harsh units, or into the simple, split-RV form, as she made it progressively fainter before ceasing to call.

In 1964 the male of the Scissor-tail's nest we watched also used the CV fairly frequently. Usually he uttered it if he was active and apparently agitated during guarding, and would give it either from a guard perch or while hovering by the nest. Usually he employed the form with a relatively faint, slightly harsh ascending arm separated by silence from a louder, simple descending arm very similar to what may be the most common form used by the female. Sometimes, while he was calling while hovering by the nest, he would utter calls which approximated the female LHV/CV (fig. 8:2d). He also had a habit of occasionally using bursts of three to about nine simple, brief harsh units in quick succession (fig. 8:3a) during flight, on taking flight, or on landing.

Similar calls were used by more than one male in 1962. They apparently reflect some sort of locomotory hesitance (although there is no accompanying WFt) as they are usually given in situations in which a male is flying away from the nest, or from a guard perch, in the absence of his mate, or is flying toward a countercalling male, or is leaving the nest region in an ambivalent situation (two females present). Further, they sometimes occur immediately before or after an

LHV. In other words, this brief, harsh call may have both locomotory hesitance and anxiety aspects to its message — perhaps among other things. It would not be surprising, for instance, if it also encoded an aggressive aspect, since the call occurred in most of the fights either the male or the female had with the House Sparrows.

This brief, harsh unit is one of the most interesting calls used by the species. It serves to draw attention to the fact that none of the calls I have described can confidently be called a CV; they are mostly simple, faint, and repeated in rapid series in situations which have much in common with the situations of CV usage in other species; but they also bear hints of more complex messages than are usual for a CV. I can see, however, no simple way of naming this intergrading complex of vocalizations in a fashion that will permit comparison with the other species and yet indicate the close association of these calls with one another. From their usage it is clear that, among the calls now known, these are as close an approximation to CV as the species has in its repertoire, and until they are better known they may as well reside in this pigeon hole.

Regularly Repeated Vocalization

Division of the RRV of *T. forficatus* into phrases varies among individuals. Some birds fairly consistently utter a brief string of RV units, perhaps ending with a couplet, and then pause and either repeat this or go on to their more complex final phrase. Other individuals simply begin a series of RV units and proceed without pause to the complex ending of the RRV. While the introductory portions vary considerably even within the delivery of any single individual, the final portions vary much less but differ among individuals. Typically, the terminal portion begins with an RV or with one or two two-peaked elements (as shown in fig. 8:3c), and then has one or two elements resembling RVs with tails. Then comes the final flourish, another RV-like element with an appended, high-pitched, two- or three-peaked termination.

During at least the portions of the nesting season in which I have worked, the RRV is given by each male from a site within his loosely defined territory every morning, repeated regularly and rapidly in the predawn twilight. There were no more than individual differences between calls recorded in 1962 at one site and those recorded in 1964 at another. Further, the descriptions of both Nice (1931) in Oklahoma, and Fitch (1950) in Brazos Co., Texas, suggest that their birds sounded very much like mine while calling in the same early morning hours, although Nices' bird, in what may have been post-RRV calling, added a variant or perhaps used RVs with some LHV. I have occasionally heard the RRV late in the evening twilight, as has Fitch, but it is apparently not used during the day. The RRV is also the vocalization employed in the Tumble Flight display (q.v.).

In the first few minutes after the most regular RRV usage in the morning, males begin to move around and call many RV units. Occasionally an RRV phrase is inserted into this calling, but the practice is not common for long after the post-RRV phase begins. Later, if the birds remain active and countercalling, the LHV takes the place of these occasional phrases, apparently being used as if it were a CdV (in combination with the RVs — but see under LHV).

Tumble Flight

The Scissor-tail has a flight display resembling very closely that of several species of kingbirds, although in this case it is likely that the bird does not actually "tumble." In the best cases I have seen, a male flew forward repeating the RV and then quickly built up speed, rose about 20 feet higher, stalled with the tail widely fanned, and pitched forward, falling five or more feet. At about the apex of the stall he began the final phrase of the RRV and completed this, with a Wing Whirr, while pitching forward (10 observations, one recording). I never saw clearly whether he grappled during the pitch forward, but am sure that in no case did a male engage in the violent tumbles often characteristic of the Eastern Kingbird. In most of my observations the vertical excursion preceding the stall was considerably less than 20 feet, but these same flights had up to five stalls each. Fitch (1950) also describes this display, agreeing with me on the Wing Whirr and vocalizations; the flights he described, however, were characterized by erratic directions and opening and closing of the rectrices. Such twisting and turning is often seen in kingbirds, and is probably just a variation of the display. Brandt (1940) describes the course of a bird performing this display as "zigzag" and says that in a single flight the bird mounts to about 100 feet in the air, pitches down about 25 feet with a high pitched noise that he felt included at least Bill Snapping, and then repeats this several times. Brandt also reports that on the ultimate ascent of such a flight the bird may climb vertically higher than before, then topple over backward, "making two or three consecutive reverse somersaults . . . all the while displaying to his mate the soft, effective, under-wing colors."

Most of the displays I saw were associated with territorial rivalry, and twice two males flew out in parallel and displayed nearly simultaneously. Fitch has also seen the display used by birds both going to and returning from mobbing a hawk.

Other Non-vocal Displays

A Wing Flutter display is used by both pair members in greetings along with the LHVs. Typically, the wings are held part way out from the body, with the carpals clearly visible but not far extended, and are fluttered rapidly through a very small arc at the tips; they are kept approximately along the plane of the body, not lifted above the back. During vigorous WFt the long tail is usually widely spread, and is sometimes scissored open and shut; it is apparently not quivered. Following the WFt the tail usually scissors open and shut at least once as the wings are folded. Wing Flutter also accompanies the LHV in other situations than greetings when a bird is landing and usually if the LHV is uttered while the bird is perched.

There is also a Wing Flicking display. We saw it on several occasions in 1964 when a flycatcher was facing an intruding House Sparrow, but hesitating before attacking. In the WFk the partly opened wings are flicked simultaneously upward and forward over the back while the bird faces more or less toward its adversary in a Crouch posture. (It is not certain that this Crouch is a ritualized display, as no individual we observed held it long enough for us to be sure that it was not just a balancing movement. In most instances, though, to interpret it as a balancing movement would require some stretching of the imagination, and it is very likely that there is a Crouch display, homologous with that of other members of the genus; we did not, however, see the head extended conspicuously forward and the bill pointed down). The tail was usually at least partly open during WFk, but was not flicked. There was no associated vocalization in any case. Attack usually followed, but not always immediately. WFt also often preceded attack, or occurred during fights; once the female directed a WFk display toward a House Sparrow, then shifted into WFt display, and then attacked.

In none of the several intraspecific encounters I observed in 1962, and in none of the many interspecific encounters we watched in 1964 was either RCP or RRCP noted. Nonetheless, the species has a concealed crown patch, and almost certainly does have these displays. Scissor-tails are very active, agile flycatchers, and it would be very easy to miss at least the RCP in a whirling melee, particularly when not observing through binoculars. Wing Whirrs were common in attacks, however, and in 1964 were often recorded from both male and female. There seem to be two sorts of sound, one rather high pitched, and one relatively noisy (fig. 8:3b) and not unlike the sounds many species of birds make with the vigorous wingstroke used in taking flight — probably it is not ritualized, while the higher sort is. The male usually produced both, often in sequence, but the female seemed only to produce the latter. Males also use the high Wing Whirr in the Tumble Flight display. I several times heard Bill Snapping in fights, and recorded it at least once.

Gaping was noticed only once, when a second male visited the nest site in 1964. One of the two males would approach the female in the nest and be repulsed each time as she stretched her head up and forward toward him and Gaped, uttered a short harsh vocalization, and apparently Wing Flicked. The other male would then attack the male which had approached her; this was repeated several times.

Perhaps because I was busy with other equipment and almost never watched Scissor-tails through binoculars, I saw only one other non-vocal display, and this only once. In 1962, after an encounter with an intruding pair, the female of a pair whose nest I had located, landed by her nest while I stood not far off; she called an LHV, and showed a Crown Ruffled. The display does not show on our cine film (in 1964) but the small image size on the 8 mm film would make detection difficult.

Tyrannus savana, Fork-tailed Flycatcher

T. savana is just slightly larger than *T. forficatus* and, as that bird, has an extremely elongated, V-shaped tail. It is less colorful, lacking any hint of salmon; rather, its plumage is much like that of one of the West Indian kingbirds — the underparts are white, the back is gray, and the head, wings, and tail are black or very dark brown. There is a concealed patch of bright yellow in the center of the crown. The Fork-tailed Flycatcher inhabits a much greater geographic range than the Scissor-tail, breeding as far north as central Veracruz, Oaxaca, and Tabasco in Mexico (most of its populations north of Costa Rica are local and small) and south in suitable open habitat into Patagonia and the Falkland Islands. At least its northern and southern populations are migratory.

I studied the species only briefly, in late October and early November, 1962, near Buenos Aires, Argentina. The population there was at that time in the pre-nesting stage, and as the sexes are nearly identical in appearance I was unable to make satisfactory distinctions between them in my observations. I have never allotted sufficient time to working in habitats in which this species nests at a season when I could make observations on breeding birds, so have only a fragmentary knowledge of the displays. Incidental observations were made in November, 1962, near Jujuy, Argentina; from December through February, 1963, in various parts of Brazil (always in the post-breeding season); in June and July, 1959, in the Canal Zone; and on 24 March, 1962, near Rio Hato, Panama.

I know of no life history study of *T. savana,* and only a few useful facts can be gleaned from the literature. In my experience the birds are remarkably non-vocal in the early part of the breeding season, and almost silent at other seasons; this seems to be supported by most observers. Further, all of the known vocalizations (except the AtV, which is not very different) comprise very brief, click-like sounds. I do not know to what extent the species shows territorial behavior, but it is obvious that pairs spread out over the plains, and that there are occasional aggressive encounters between birds. Davis (1940) found that in the Argentine province of Entre Rios Fork-tailed Flycatchers showed "typical" territorial behavior during the day, but that males gathered at night to roost together in the tall trees planted around *estancias*. His observations were made while many migrant conspecifics were passing through, and these may have contributed most of the communally roosting individuals. Hudson (1920) describes a period of activity in the evening in which the birds apparently stimulate each other to much displaying, but says that they do not roost communally. If the habit of males to roost communally is present in only some populations, it may vary according to features of the habitat, as I have suggested may be the case in *T. forficatus*. Certainly communal roosting is common in flocks of non-breeding birds, and the species seems to be extremely gregarious at such times.

Locomotory Hesitance Complex of Vocalizations

Because I was unable to distinguish sexes in my few observations of *T. savana* I cannot fully evaluate most of the encounters I saw between conspecific individuals. Many of these encounters were almost certainly greetings between mates, and in the breeding season birds were usually found in groups of two. In the marsh where I did most of my work, however, many individuals were present, third birds intruded on the presumed pairs, and many aggressive encounters were seen which were likely weak clashes between males.

Two different sorts of vocalizations were used with a WFt display in many instances, although the WFt was invariably present with only one. In encounters which were probably or possibly intra-pair I often recorded both of the vocalizations, and in several cases know that in a set of observations of two birds, one individual gave only one kind of call while the other used both. The simpler of the two vocalizations comprised a series of elements that appear as nearly vertical (actually slanting slightly upward) thin lines on a sonagram (fig. 8:4b and 8:5a) with only a hint of broadening in the upper portion. These elements vary from 0.03 to 0.2 seconds apart within my sample, and the series maintain continuity only when the rate of repetition is relatively high. The second vocalization comprises series of bursts of lower frequency elements (fig. 8:4a) which are again nearly vertical, but appear to angle slightly downward and are not usually broadest in their upper portions. The bursts have from two to about six elements each (usually from four to six in rapid calling) and are about 0.05 seconds apart when in a continuous series. This sort of vocalization sounds relatively harsh. Both sorts often vary sinusoidally in frequency through the series, but this is more prominent in the simpler call.

The harsher vocalization of *T. savana* was usually used more extensively by the individual which more often employed the call I take to be the RV while perched. On the other hand, the bird using the simpler vocalization was sometimes the more persistently vocal member of an apparent pair, and would call (using series which were neither continuous nor rapid) while flycatching even when relatively far from the silent, presumed mate. This makes it difficult to guess which individual was the male, but in some cases I was able to determine that the bird using the RRV was the individual which did not use the simpler call. Thus I offer the following tentative interpretation of the events in an encounter between apparent mates: the female returns from a flycatching flight uttering occasional elements of the simpler sort, and begins to make a coherent series of these as she gets close to her mate. He then begins a harsh series, with WFt, and as she lands she too utters this call (but usually at a slightly higher frequency) with WFt, but after the male finishes calling, the female gives a final series of the higher, simpler elements. Knowing that females of other species of this genus often substitute CV for LHV in greetings, or at least pass from an LHV to a CV during a greeting when going to their nests, I am inclined to suspect that the simpler, high pitched series is the CV of this species. Having made no observations at nests, however, I have not encountered it in any other situation and cannot be sure of this interpretation. It is at any rate clear that the harsher (second) call is an LHV, and that it is used by both sexes, although more continuously by one of them.

Sometimes the LHV (the harsh call) is used in encounters that appear relatively aggressive, during which the birds may meet face to face in the air. In such cases, both individuals use the same call. In the few more vigorous intraspecific fights I have seen, the calls comprised briefer bursts not arranged in series (ILHV ?).

Brief Vocalizations

Perched *T. savana* individuals sometimes utter an extremely brief, single element vocalization which sounds like "tk." It covers a wide spread of frequencies, and is shaped like an extremely narrow "V" (fig. 8:5b). This may be the Repeated Vocalization of the species. It was sometimes given in response to calls of another individual in situations which seemed to be countercalling, and was sometimes given by a bird while its apparent mate flycaught, if the mate was repeating sporadic elements of the high LHV. This brief "tk" is also given at times in flight — by an individual following an apparent mate in some cases, and by the bird returning from mobbing an owl.

A second brief call, also usually covering a wide spread of frequencies but comprising two or three elements (fig. 8:5c) is also heard occasionally, and is more likely to be repeated at a higher rate than is the "tk." Sometimes a few such bursts would follow the "tk" of a perched bird, and the bursts might coincide with Tail Flicking. This was the case at least once when I was observing what I took to be two males countercalling, with the mate of one perched silently nearby. A few bursts of this call sometimes precede flight, and bursts have occurred in some of the intraspecific fights I've watched. The elements of this vocalization appear to be the downstroke of a chevron or of a "V" — that is, they are like the elements of an LHV, which suggests that this vocalization is an ILHV.

Attack Vocalization

Recordings made of a Fork-tailed Flycatcher as it mobbed a fleeing Tropical Screech Owl (*Otus choliba*) reveal harsh vocalizations similar in general form to the unit bursts of an LHV. The frequency of these AtVs is higher, though, and each unit has a much greater frequency spread than an LHV unit. Furthermore, the bursts were not separated into discrete elements (fig. 8:5d) but looked more like the harsh AtVs of other members of the genus. Bill Snaps were used immediately after each unit, and a noisy Wing Whirr tended to occur at about the same time, as the flycatcher made close approaches to the owl. The wing sound was spread over a wide range of frequencies, and may not be equivalent to the ritualized form known from other species.

The AtV is quite likely the call I heard from a member of a nonbreeding flock of Fork-tailed Flycatchers in the Canal Zone on 2 July, 1959, when the bird was chased by a *Tyrannus melancholicus* which had been feeding in the same fruiting palms. I did not hear any other calls from this flock, even during brief squabbles between its members. I have also found other flocks usually silent even during brief clashes, but have heard occasional harsh notes, perhaps the AtV, in some aerial fights.

Occasional harsh bursts occur in greetings, and are uttered by the individual which also uses the higher call (the possible CV), and are also likely AtVs, as they comprise continuous sound rather than discrete elements. As the birds I was observing and recording near Buenos Aires were only recently back on the breeding grounds and behaving quite aggressively, the occurrence in greetings of an occasional AtV by a presumed female as she landed near her displaying mate is not surprising.

Note that the form of this vocalization makes it distinct within the repertoire of the species. Scissor-tailed Flycatchers also use harsh calls in aggressive encounters, but I refrained from naming an AtV in that species because the same (or very similar) harsh calls were of a very wide occurrence.

Regularly Repeated Vocalization

In examples of this vocalization recorded from near Buenos Aires and near Jujuy, Argentina, there is close agreement as to form. A series of 13 to about 26 simple elements, spaced about 0.08 seconds apart, and beginning with several relatively high-pitched elements precedes a burst of about four to eight closely packed elements. This burst is about 0.05 to 0.12 seconds in duration, sounds harsh, and is followed by two brief terminal elements (fig. 8:6a). The whole RRV sounds like a rapid rattle of clicks terminating in a harsh sound, and is repeated over and over in the predawn twilight in the fashion typical of the genus. In Panama in 1962, seven months before working with the species in Argentina, I heard but was unable to record an RRV from a bird in the Rio Hato region. From my notes it is apparent that this bird alternated two phrases, the first more or less of the above pattern and the second with three terminal bursts, rather than one. Further, it seems that the terminal portions sounded higher pitched than the introductory series of clicks, suggesting that the RRV of Panamanian birds may be rather different from that recorded in Argentina, although of the same general pattern.

On 7 November 1962, at my site in the marsh near Buenos Aires, I witnessed a vigorous intraspecific fight, apparently between two males. After the fight the birds separated and began calling abbreviated RRVs, one from a perch, and the other at first in flight, and then from a perch. These calls were much shorter than full RRVs, and had only from two to six introductory clicks preceding the harsh burst (fig. 8:6b). The two individuals began to fight a second time, and again broke apart and countercalled in this fashion. A few other birds in the immediate region began to use full RRV. On the morning of 31 October, 1962, after the owl was mobbed and driven out, all of the apparent males within earshot began the RRV again (it was by then about 0700) and kept it up as strongly as in the predawn twilight for several minutes. My one other observation of this vocalization being used after sunrise was made in the Territory of Amapa in Brazil on 7 February, 1963, when a bird flew to within two feet of another, faced partly toward it, and repeated the RRV three times before the second individual flew away; the time was 0710. These several observations would suggest that use of the RRV after sunrise is not uncommon, although it is not known whether the abbreviated form heard in the intraspecific encounter should be considered an RRV or a related display.

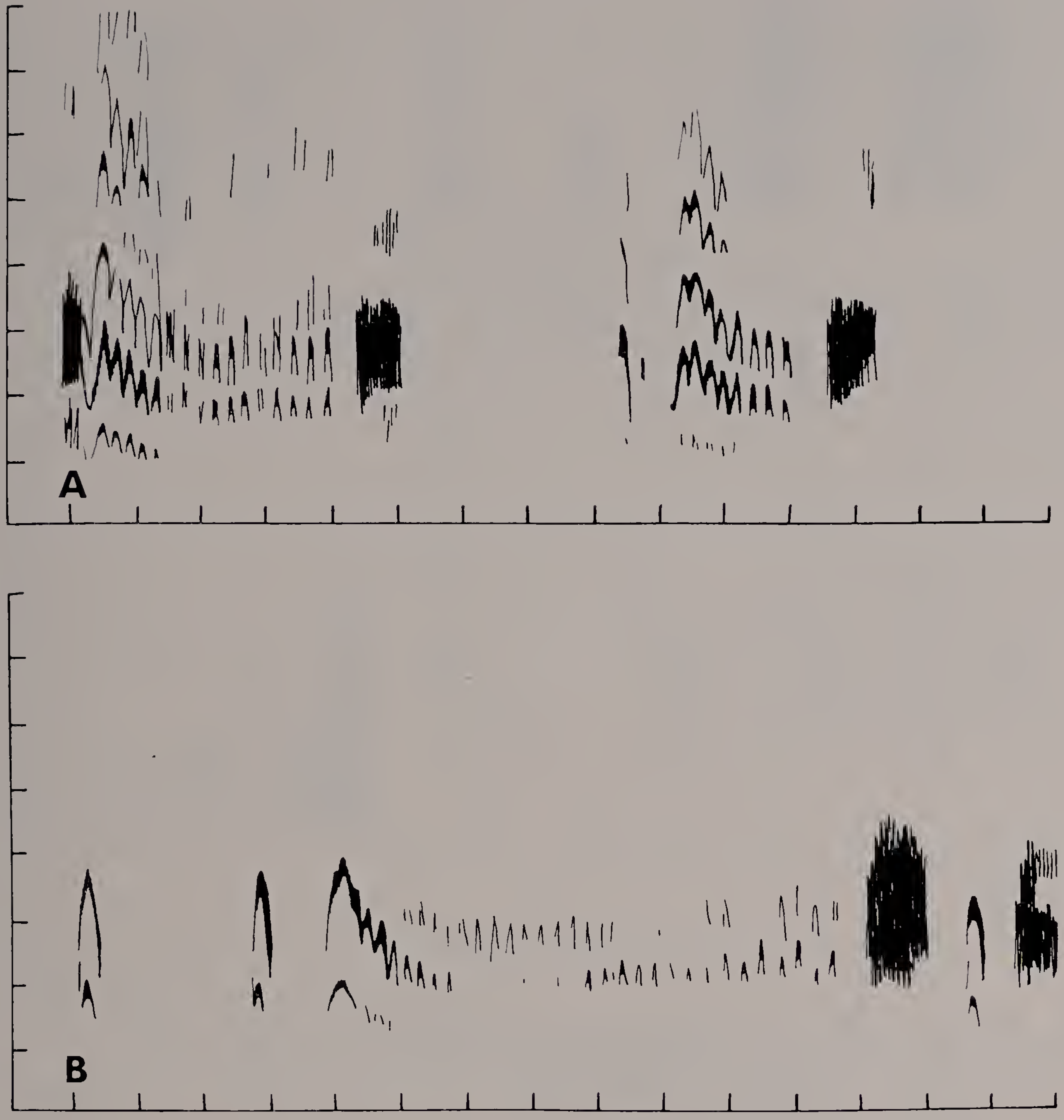
Tumble Flight

I have not seen the Tumble Flight display in *T. savana*, and know of no account which is an unequivocal description of it. Hudson's description (1920, p. 192) of the evening activities of Fork-tailed Flycatchers, however, almost certainly does refer to a display of this sort. Just before sunset his birds would apparently perch on tree tops and countercall "with loud, excited chirps" (perhaps the call I have described as "tk" and think may be the RV). Eventually they would fly rapidly to "a great height in the air; then, after whirling about for a few moments, they precipitate themselves downwards with great violence, opening and shutting their tails during their wild zig-zag flight, and uttering a succession of sharp, grinding notes." Such erratic zig-zag flights are often seen in Tumble Flight displays (and particularly in a form in which the bird does not tumble, although sometimes in the complete display) of kingbirds. The calls Hudson describes are apparently different from the LHV (which he calls "rattling castanet notes") and may well be the terminal portions of the RRV. Hussey (1916, p. 394) working in the same region, also saw what were apparently similar performances "at sunset" and presents a less detailed description.

Other Non-vocal Displays

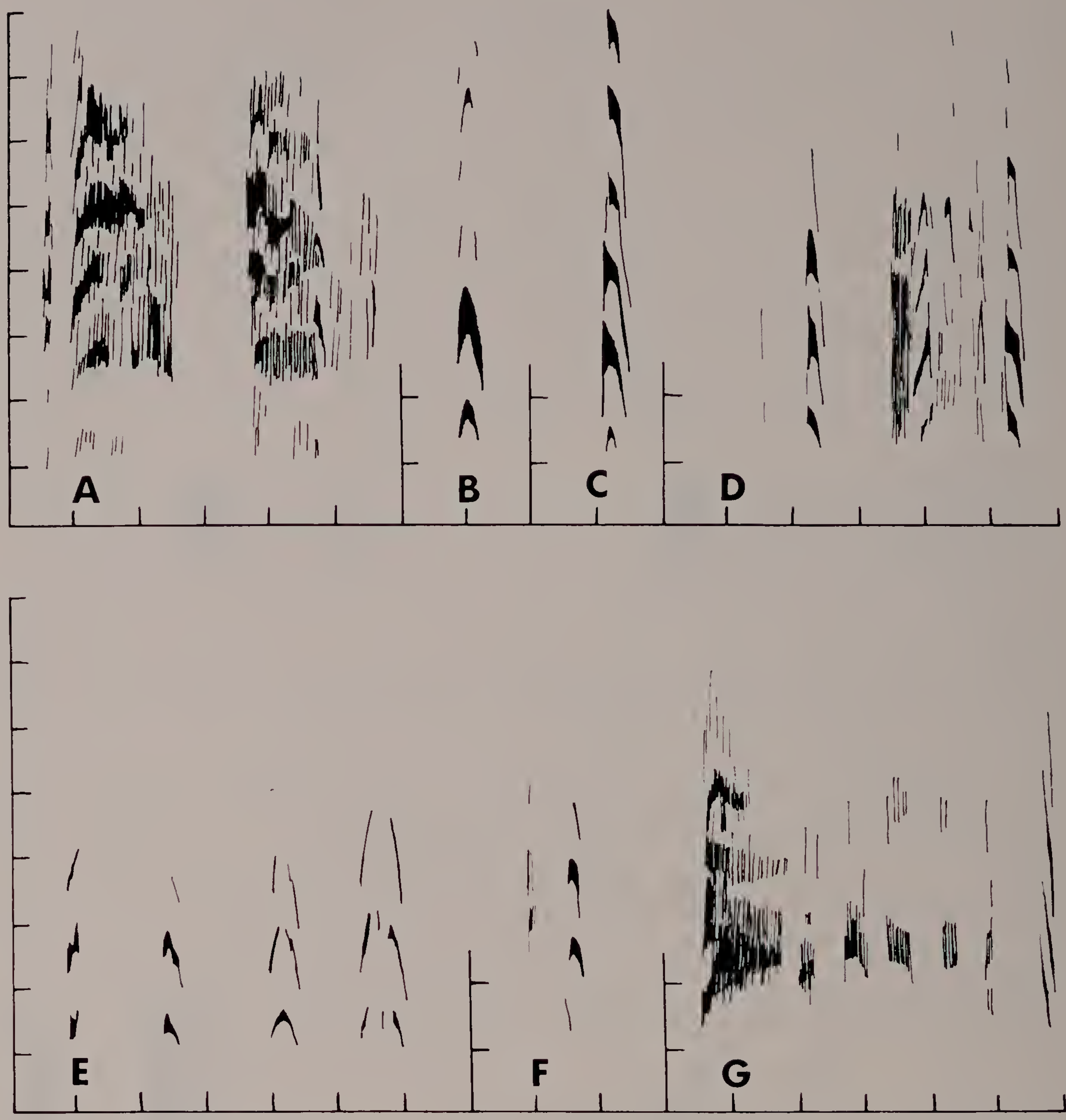
A Wing Flutter display in *T. savana* has already been mentioned as accompanying the LHV(s); it looks very much like the WFt of *T. forficatus.* No Wing Flicking or Tail Quivering are known, but Tail Flicking has been seen at least twice by a bird just before taking flight to attack a conspecific, and twice (see below) by a bird which did not fly. No Crouch has been identified. I have seen both Head Ruffled and Revealed Crown Patch, both in non-breeding flocks of birds feeding together in the Canal Zone in June and July, 1959. The RCP was used by a perched bird in each case, along with Tail Flicking, but with no vocalizations and with no overt signs of engaging in social activity. In both instances there had been some silent squabbling between individuals of the flock, although I had not seen the displaying individual involved. That I have seen so few displays in *T. savana* during the breeding season may be in large part attributable to my preoccupation with tape recording.

Figures



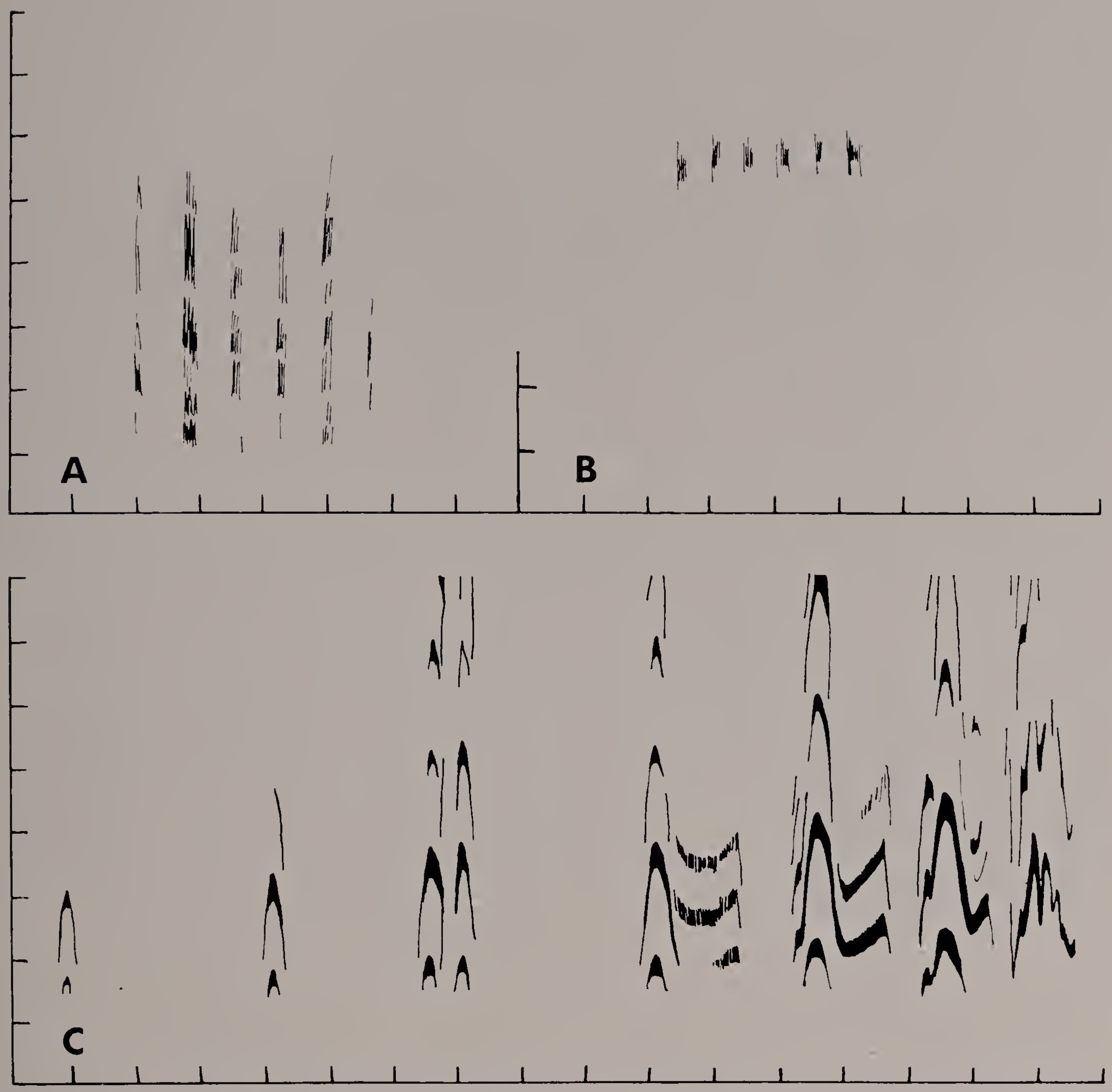
Tyrannus forficatus

Figure 8:1a. Two consecutive LHVs by a male greeting his mate.
8:1b. An LHV by a perched male, without WFt, in post RRV counter-calling. It was preceded by four RVs, the last two of which appear in the figure.



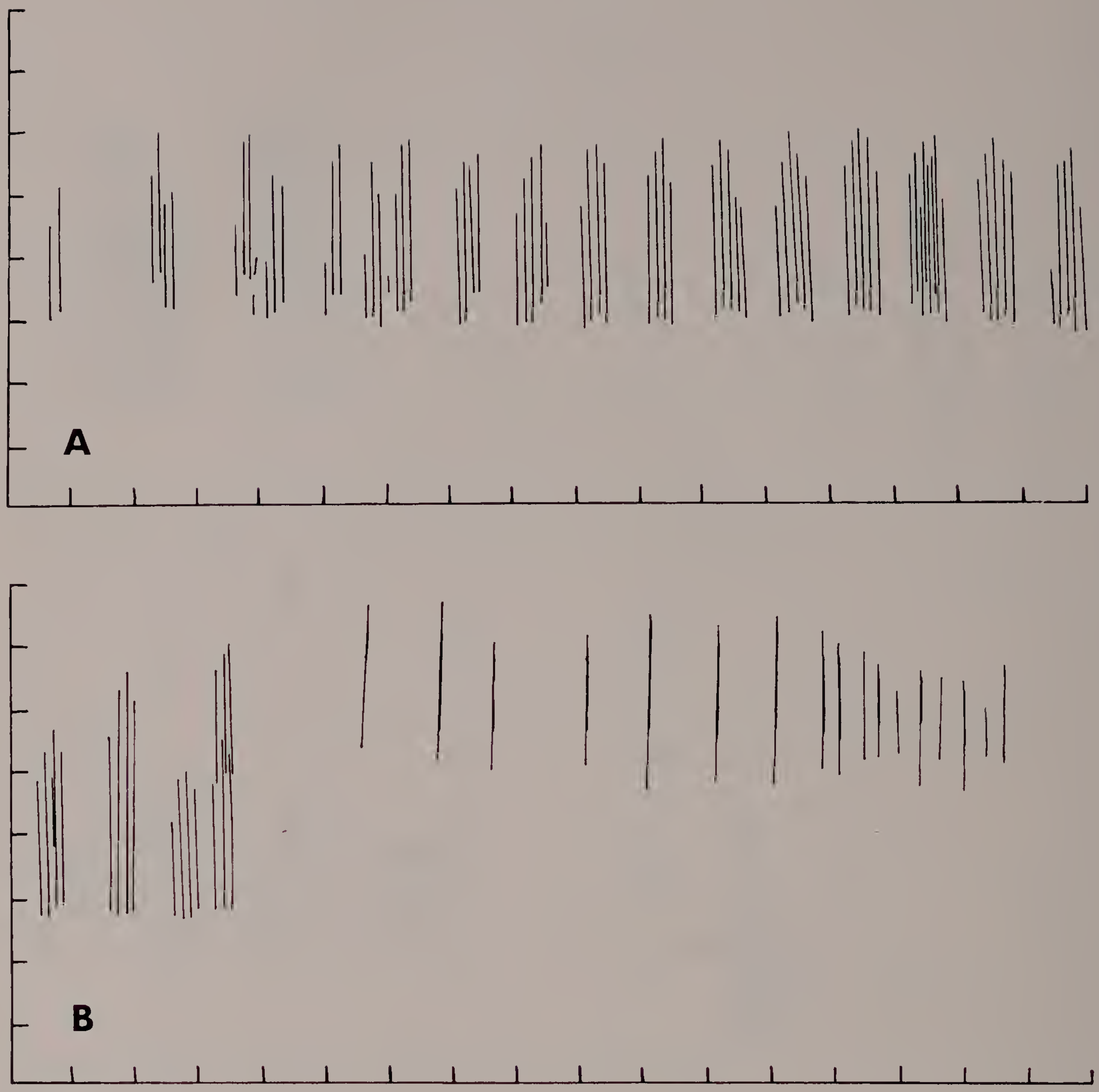
Tyrannus forficatus

FIGURE 8:2a. Two units of a female LHV.
8:2b. A nearly symmetrical RV.
8:2c. An asymmetrical RV.
8:2d. Portion of an odd male CV showing some relationship to form of female LHV.
8:2e. Simple units of CV (by a female, units consecutive).
8:2f. A CV unit (by female) with a weak ascending arm and louder descending arm.
8:2g. Portion of a female CV with LHV form.



Tyrannus forficatus

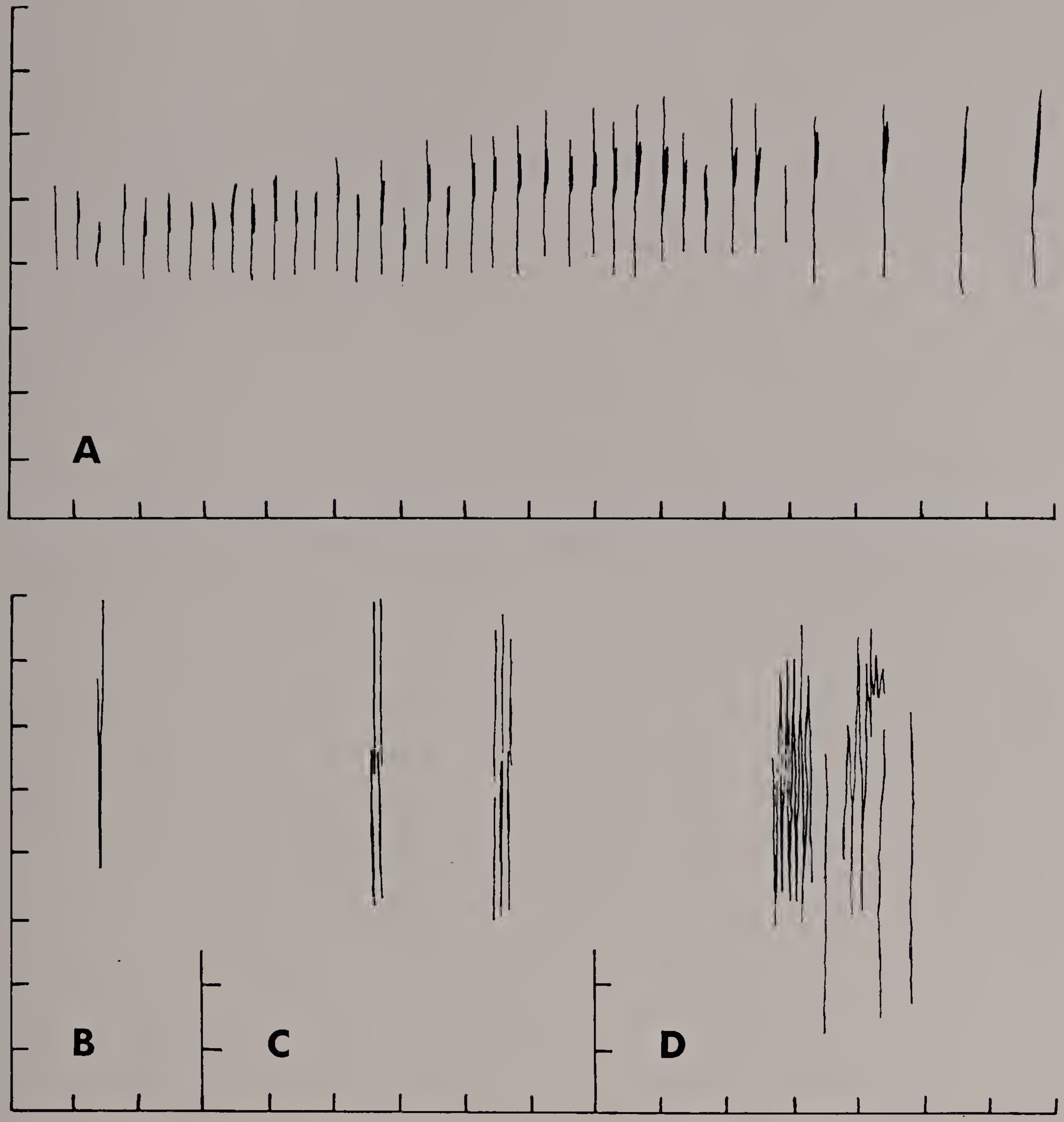
FIGURE 8:3a. Call of male in flight.
8:3b. High pitched Wing Whirr of male fighting with a House Sparrow.
8:3c. RRV—the example is a relatively brief one, not clearly divided into phrases, and lacking many introductory RV units.



Tyrannus savana

FIGURE 8:4a. Harsh LHV from both members of a pair. One flew and its apparent mate followed, the first bird turned and they met in air, gave these calls with WFt, and separated. Continuous with 8:4b.

8:4b. End of harsh LHV by pair, one bird changes to simpler LHV or CV. Continuous with 8:4a.



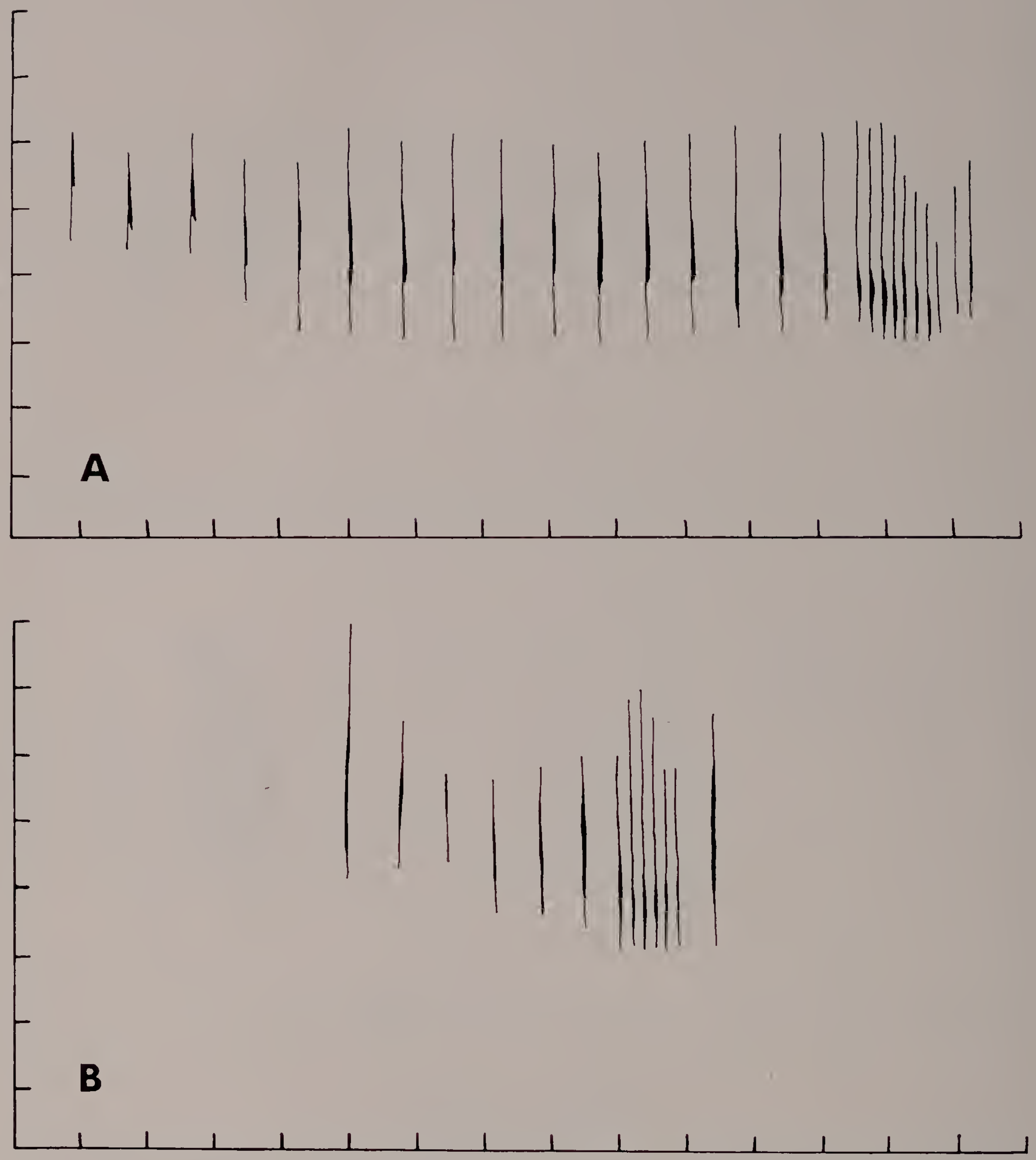
Tyrannus savana

FIGURE 8:5a. Portion of call of presumed female flying with WFt and being followed by presumed mate, who did not use WFt and called only an occasional harsh LHV burst (none during portion shown here). This vocalization may be CV or a simple form of LHV.

8:5b. Probable RV, by a perched bird.

8:5c. Two probable ILHVs by a perched bird. Given with Tail Flicks.

8:5d. Two AtVs and three Bill Snaps by a bird attacking a flying owl.



Tyrannus savana

FIGURE 8:6a. RRV.
8:6b. Abbreviated RRV given in countercalling after a fight.

RELATIONSHIPS AND DISCUSSION

Chapter 9.

ZOOSEMIOTIC COMPARISON

Many of the zoosemiotic conclusions of this study were presented in Chapter 3, where I attempted to show how the displays of *T. tyrannus* mediate the functioning of the social organization of that species. That discussion dealt with the messages and meanings (or the hypothetical states preceding observable meanings) which I feel can be inferred from what is known at present of the displays of that one species. I shall not repeat that material here, and shall not make similar analyses for each of the other species — such an exercise would contribute little to the views already expressed. Rather, this chapter deals with a different topic, the kinds of zoosemiotic comparisons that are possible when one knows something about the display repertoires of the different species. For this purpose, the discussion in Chapter 3 is a necessary precursor and complement; the two sections together contain all of the zoosemiotic discussion of this study.

A fundamental difficulty arises when one attempts to compare the repertoires of different species, as it seems that the calls of no two species match exactly. Each species has slightly or considerably different ways of "slicing the message cake;" that is, of dividing up what may be a multi-dimensional continuum of socially relevant messages. Thus, one problem has been to find criteria for naming the displays which would make the different repertoires easily comparable in the absence of exact equivalences in either message or form. Further, in the absence of full information about the usage of each display, the ranges of variation, and, in some species, the extent of the repertoire, any attempt at categorizing must be regarded as being to some degree provisional. In particular, I have found it difficult to compare the displays of some species with the ILHV and CdV of *T. tyrannus* when there is not a close matching of RV messages. Primarily because of lack of full information, I have settled rather arbitrarily on the following criteria for categorizing, even though I strongly suspect they will prove inadequate.

(1) Calls used in greetings are presumed to include the LHVs of each species, and, in some cases, CVs by females.

(2) Chattering calls used by apparently anxious females in or near their nests are presumed to be CVs. (Note that this involves criteria of both usage and form.)

(3) Calls used in countercalling are taken to be RV (RHV in some cases), CdV, or RRV. RRV is distinguished from the others by being regularly repeated in the predawn twilight and not usually

at other times of day (some exceptions, not including the Tumble Flights of several species).

(4) The ILHV is presumed to be used primarily by birds that are unlikely to be aggressive (or aggressive without showing obvious signs of fear); ILHV thus should not be much used in counter-calling and, on the whole, should be rare relative to the RV. Its message is surely only partly understood as yet. The ILHV category is not always applicable, hence some species have an RHV category.

(5) AtV and AeV are recognized solely on the basis of their usage and their relative distinctness from other calls in each species' repertoire.

(6) Non-vocal displays are recognized on the basis of form, or, in the case of sounds, method of production.

(7) Comparison with the repertoire of *T. tyrannus* has not been used as the sole method of categorizing; decisions have been made about what to include in each display with respect to the position of that display in the unique repertoire of the species under consideration.

All of the species of *Tyrannus* appear to have repertoires which are in many ways similar, and which serve similar ends in the annual behavioral cycle of the species. Sufficient information now exists to enable us to recognize features which are general and some which are not, and to help us identify necessary directions for future research. The following presentation is organized first around a discussion of the displays, presented in sequence, then of characteristics of the repertoires. A phylogenetic comparison is reserved for Chapter 11.

Comparison by Displays

Locomotory Hesitance Complex of Vocalizations

In most species the usual form for the LHVs uttered by males is a prolonged series of repeated elements or compound units; this may be followed by shorter but similar calls, or these shorter calls may be used without the prolonged form if the situation is not particularly intense. In at least *T. tyrannus, T. melancholicus, T. albogularis, T. dominicensis,* and *T. savana* males and females often use closely similar forms, the females' being usually at least slightly shorter and often lower pitched. Females of these species also have more variable shorter forms, and at least some of these terminate in high peaked elements, perhaps related to AeVs. In the other species, so far as is known at present, females have only relatively short LHVs, which can be repeated but which don't usually form continuous series, and these always comprise high peaked elements or units. In *T. dominicensis* both sexes usually utter a set of bursts, and really prolonged series seem at least relatively uncommon — although they may be used by either sex. This case is perhaps phylogenetically related to the LHV forms of male *T. caudifasciatus* and of *T. tyrannus,* in both of which the long series are made up of a succession of patterned shorter bursts, rather than a succession of closely similar elements as in most other species. It is this repetition of a complex and variable unit that gives *T. tyrannus* one of the most complex LHVs in the genus.

The basic message of the LHV seems to be one of interference with a tendency to locomote, although this is relatively certain only in the few species for which there is now extensive information on usage. The higher peaked, short female LHVs at least must have other elements in their messages, and it may be that "locomotory hesitance" is not the basic common denominator of message in female LHVs. This problem is hard to study, however, as females are much less vocal than males in most situations. Further, females rarely use their LHVs outside the greeting situation, other than sometimes when flying from the nest. It may be that when more is known about the female forms and their usages the LHV category will be seen to comprise unlike entities, and that some will need distinct names.

Where sufficient is known about a species' use of the LHV, at least the male form is most commonly uttered with the WFt in situations characterized by indecision and locomotory hesitance. In some species, and perhaps rarely in all, it may be given during countercalling without the WFt and when no evidence of locomotory hesitance is observed. This is most prominent in *T. verticalis* and *T. vociferans,* both species in which there is a relatively small difference in form between the LHV and the CdV, and in *T. forficatus,* which does not seem to have a CdV.

Incipient Locomotory Hesitance Vocalizations, Repeated Vocalizations, and Related Forms

It is difficult to see a pattern of form within the genus for these vocalizations, and it is also difficult to interpret in detail their messages and functions. Probably all include a message of at least some degree of locomotory hesitance, and perhaps each specifies to some extent a different sort of hesitance. The brunt of species and perhaps individual identification probably falls on these short calls during the daylight hours in which they supply most of the monitoring information to conspecifics. The RV indicates a relatively greater probability of the communicator becoming aggressive than does the ILHV, while the latter may usually indicate a potentially more dangerous situation. The message of general discomfort, which is apparently encoded by the ILHVs of at least fledgling *T. tyrannus* and *T. melancholicus,* ceases on the whole to be socially relevant once the young are independent.

What vestiges of the message remain are likely allotted to the CV, a call the young do not use.

Species Summary. The ILHVs of *T. savana* and *T. tyrannus* are more or less similar to the units of the LHVs of these species; this may also be true for *T. caudifasciatus*, although the ILHV has not been surely identified, and *T. dominicensis* apparently uses a much abbreviated LHV as its ILHV. *T. melancholicus* and *T. albogularis* both have simple series LHVs which could be abbreviated to form ILHVs, but apparently are not, and the ILHVs are of different form from the LHVs. *T. verticalis* also apparently has an ILHV which is unlike the form of its LHV. The repertoires of *T. crassirostris* and *T. niveigularis* are as yet too poorly known, but that of *T. forficatus* is better known and apparently has no ILHV. *T. vociferans* does not seem to have a call that corresponds closely to the ILHV, but the message is somehow divided between two other vocalizations, one of which does resemble an LHV unit. Finally, in *T. couchii* the ILHV is not like the LHV unit, and the call apparently overlaps in message with the CV of *T. tyrannus.*

The RV is in most species quite distinct in form from the ILHV, although this does not seem to hold in *T. vociferans.* In that species the two calls which exist (RHV and what is essentially an abbreviated version of it with a different range of variation, the SRHV) seem to overlap considerably in usage. *T. forficatus* and *T. verticalis* apparently have simple, chevron-shaped RVs, and these species have highly variable but primarily harsh CVs. *T. tyrannus*, on the other hand, has a harsh and variable RV and a relatively invariant CV comprising chevron elements. In *T couchii* where the chevron-shaped call is an ILHV, the CV is highly variable and mostly harsh, and there is no RV but an RHV. The RV of *T. savana* is apparently an inverted, narrow chevron (no CV is known). RVs comprising series of elements occur in at least *T. melancholicus* and *T. dominicensis*, and are quite similar in form.

Compound Vocalizations

Compound Vocalizations apparently always relate to some other vocalization(s) in each repertoire, and there seem, on the whole, to be two main sorts of relationship. In one case the CdV relates, through compounding, to a CV and an RV or perhaps an ILHV, and in the other, with no apparent compounding, to an LHV. Granted the relationship of LHV to both ILHV and to CV (a call which can, in some greetings, replace an LHV), this is perhaps not surprising. Nonetheless, some degree of difference in messages is involved, while the function of the CdV seems likely to be comparable throughout the genus. In all species where it is known, the CdV seems to indicate a high state of readiness to defend, but also a considerable inhibition and perhaps anxiety.

Species Summary. In *T. tyrannus* the CdV appears to be compounded of a CV plus an RV, or, rarely, plus an ILHV. In *T. caudifasciatus* it appears to be compounded of a CV plus some other vocalization — but neither RV nor ILHV are yet known in this species. In *T. crassirostris* if it is compounded at all it is of an RV or ILHV and some brief harsh units which might be either LHV or an unknown form of CV. In *T. couchii* it appears not to be compounded, but merely an extended RHV — with, however, occasional dissociation of the terminal portion, which suggests that a CV may have been involved. The CdV is very like the LHV in *T. verticalis* and *T. vociferans*, and the two displays often intergrade completely and are to some extent used interchangeably. The CdV and the LHV or ILHV are also alike in *T. dominicensis,* but this is hard to evaluate as all of the vocalizations of this species comprise series of fairly simple elements with a more prolonged element at or near the start. It would perhaps be as satisfactory to consider the CdV as an RV preceded by one or a few CV units in this species, although in this comparison the elements following the prolonged element are dissimilar. In *T. melancholicus* and *T. albogularis* there is too little evidence yet to identify the CdV, but the best candidates are like extended ILHVs with a few associated brief, harsh elements.

Chatter Vocalizations

In all species, the CV apparently carries a message of anxiety in situations which may require defense of self, nest, or territory. It seems to be possible to express not just anxiety, but a relative readiness to defend *vs.* a more fearful mood. Sometimes these finer distinctions are made by employing variations of the CV, and sometimes the CV carries only some of the possible messages, while another display, usually the RV, carries the others. At least some species give indication that a range of variability has been available in the evolution of the CV and RV, and that the extent to which one has gained or lost part of this range has influenced the evolution of form and usage in the other, or in some cases in the ILHV as well.

Species Summary. The CV of *T. tyrannus* is almost always a simple chevron, while the RV is a more prolonged, very harsh call, and the ILHV might be thought of as sharing aspects of both in a sequential combination. Very brief, harsh calls occur in attacks and fights, but these seem to be variations of the RV toward brevity, which makes it more CV-like. Harsh variants of the LHV of this species become like harsh CV series but, again, seem to be related more to the LHV than the CV; in short, the CV itself seems to have lost certain forms to these other displays.

In *T. verticalis* it is apparently the RV which is a simple, relatively invariant chevron while the CV is more prolonged, very variable, and integrades with ILHV. Similarly, in *T. forficatus* the RV is chevron-shaped, but here it is more obviously variable, and its asymmetrical forms apparently encode more anxiety. This species seems to lack an ILHV, and its CV is incredibly variable.

The simple chevron again recurs in *T. couchii*, now as an ILHV with a markedly anxious aspect of message, and the more defensive messages are in the RHV and the variable CV. *T. vociferans* seems to be unusual in having a rare CV and no ILHV-RV distinction; its RHV and SRHV are both extensively variable, and either may give rise to faint, chattering calls which are apparently CV.

The only other species for which I have nearly sufficient information are *T. melancholicus* and *T. dominicensis*. The former has both simple and harsh CV forms (the harsh occurring at least at the termination of a prolonged female LHV) and can probably span the message continuum from relatively ready to defend to relatively fearful. Its RV contains both sorts of form in different elements, and its apparent ILHV comprises solely simple elements. All of the CVs I have recorded from *T. dominicensis* have been slightly harsh, suggesting that they might be able to vary in either direction from this more or less mid-point. The RV of this species is similar to that of *T. melancholicus*.

Attack and Attackee Vocalizations

The status of these categories is very much open to question. The AtV is simply a very harsh call, given by an attacking bird; it may appear to be an intermediate between a harsh CV and an RV, between a CV and a harsh RV, or may be just a harsh form of the LHV (as in *T. dominicensis* and, perhaps, *T. melancholicus*). What seems to be general is that it must be harsh, having either very rapid fluctuation of frequency over a wide range, or a tendency to form at least three peaks in each elongate unit of the vocalization, or both. There may be no AtV as such, but merely a continuously scaled variation which can be applied to some or any other vocal display.

Even less is known about the AeV. Birds under attack sometimes are heard to utter quite high pitched vocalizations, some of which may achieve a standardized form. Usually these vocalizations seem to be derived from either the ILHV or LHV form. In one case, *T. tyrannus*, the AeV resembles quite closely the terminal portion of the RRV, and it is the AeV which in this species occurs in the Tumble Flight display.

Regularly Repeated Vocalizations

The RRVs of most members of the genus are recognized quite readily in the field by the pattern they have in common — a hesitant, rhythmless series of elements building to a flourish that usually sounds relatively complex. The amount and elaboration of the hesitant portion, as well as its continuity or division into "phrases," varies among individuals and to a lesser degree within the performances of any one bird. The whole RRV is repeated, often with striking regularity, as a unit during the predawn twilight. Such regular and prolonged performances almost never occur after sunrise, although some species characteristically give shorter regular or irregular performances during the day or night, and at least the "complex" portion of the vocalization is used by most species in their Tumble Flight displays.

If regular repetition is taken to be a characteristic of this display, then the fact that some individuals customarily repeat it only irregularly must be explained. The RRV may function to attract females to unmated males, to establish relationships between neighboring males, and to maintain these relationships. Such maintenance may require constant reaffirmation in dense populations, but may be quite unnecessary if there are no near neighbors and nothing to reaffirm. This may explain why irregular repetition or even omission of the RRV is unusual in dense populations of a species in either the temperate regions or the tropics, but is fairly common in very sparse populations. It may or may not fully explain, however, why irregular repetition or omission of the RRV seems on the whole more common in the tropics than in temperate regions. In tropical areas where there are resident populations, though, it may be usual for adults to remain mated at all seasons so that there is rarely need to attract a mate, or to compete with neighbors who are also forming pair bonds.

The form of the RRV is now known for all species except *T. cubensis*, *T. albogularis*, and *T. niveigularis*, and for the last I have a recording of a flight display call which is probably an RRV or a simplified form of it. Figure 9:1 presents a diagrammatic representation of RRVs from selected individuals, so arranged as to align vertically (in so far as possible) similar elements or groups. These aligned portions might be homologous, but in many cases may instead be elements of different origins pressed to fill out similar sections of the RRV pattern typical of the genus. In some cases different alignments seemed about as likely, but to keep the diagram simple I arbitrarily chose to represent only one possibility per species. As examples of such cases, the element labeled C_1 of *T. crassirostris* might well belong to a C_3 group, the group of brief elements which follow it might be an elaborate C_4, and the species might have lost elements C_1 and C_2. Similarly, the flight display call of *T. niveigularis* should perhaps all be arranged from C_1 to C_4 instead of split as I have it. Neither the different alignments I can visualize nor the uncertainty as to homologies, however, interfere with the main feature that can be read from this diagram.

The horizontal dividing lines of fig. 9:1 separate the species into the four geographic groupings followed in the organization of the chapters of Part II: the western North American and Mexican species, the Central and South American species, the West Indian species (plus *T. tyrannus*), and the possible subgenus *Muscivora*. Within each of these four subdivisions (except the last, which is obscured by the reduction of form in the elements of *T. savana*) the RRVs have more characteristics in common than they share with species in any of the other groups. The first group is the most complex, and it is more difficult to align than are the other groups, but for each of its stranger elements the most similar element in another species is found within this first group. Further, the impression one gets on hearing the RRV of *T. caudifasciatus* is that it is unlike that of other kingbirds in so many characteristics that its relationship to them might be questioned. Undoubtedly *T. caudifasciatus* is an atypical kingbird in many respects, but when the elements of the RRV are segmented as in the diagram their similarities to the corresponding elements in *T. dominicensis* become apparent. There also seems to be a general similarity between the RRVs of *T. caudifasciatus* and *T. tyrannus*.

Tumble Flight

Probably all members of the genus *Tyrannus* have a flight display, although it is not yet known in several species. The "tumbling," which appears to be ritualized fighting behavior *in vacuo* (in the sense that there is no opponent close enough to grapple) has not been seen in all of the species that have an aerial display, and occurs in only a fraction of the flights of those species where it is known. Less "complete" versions typically include erratic twisting and/or repetitive stalling. *T. forficatus* may substitute a dive or a backward somersault for the tumble. Wing Whirrs are commonly used at the onset of the tumbling portion, and bear a specific relation to the vocalization in at least *T. verticalis* and *T. vociferans*. The vocalization is usually the RRV or its complex portion, or is closely related to it. In *T. tyrannus* the vocalization is an AeV, but the form of this is closely similar to the terminal portion of the RRV of that species.

The message of the Tumble Flight is probably that a very strong aggressive tendency is being inhibited or frustrated.

The display apparently at times is a substitute for fighting, as in several species cases have been seen in which two males have flown out simultaneously on parallel courses and both have performed. Only one observation has been made (in *T. dominicensis*) of one bird actually striking another during a flight in which both of them performed, and this did not lead to either a full fight or a full rout while the two were in sight. In other cases, while displaying birds did not align with one another, it was obvious that the display was infectious, and after one had displayed, all of his neighbors would fly up and perform in kind. At Delta such "infection" extended in both directions between the two species *T. tyrannus* and *T. verticalis* despite differences in the vocalizations used by each. This *may* have been due to the relatively recent overlap of their ranges locally (although I do not know if they behave similarly elsewhere). At the townsite of Portal, Arizona, where *T. verticalis* and *T. vociferans* were both present at an unusually high density, *T. vociferans* displays were not seen to cause *T. verticalis* to follow suit (the latter was not seen using this display during my observations at that site).

Other Non-vocal Displays

While the presence of the remaining displays has not in all cases been established for all species, what is known suggests that most or all are held in common, and are in form little different from their counterparts in *T. tyrannus.* Whether or not they have the same ranges of message in each species is less clear, as many observations are required to determine this.

One activity which I have described may be a display, and may occur widely in the genus, but I have not seen it often enough to be sure of either. It is what I have called male nest site showing, or female nest site prospecting. The latter, at least, is quite possibly a functional activity in its own right, but as the male does not build, his activity is almost certainly display. Both sexes utter CVs while performing. In many ways the behavior is quite similar to something that Johnson (1963) has described as a "solicitation display" in *Empidonax*, another tyrannid genus, and even the vocalizations used by the two genera seem to be similar.

Finally, it is worth noting that there is apparently no precopulatory display, although a display of this sort seems to be fairly widespread in other birds studied. Females ready to copulate will at times approach males and crouch before them, and males usually respond by simply mounting. At times males apparently mistake an aggressive Crouch display of a female for this posture, and at times males will attempt to copulate with mates who are crouched in the nest. Frequently males attempt to mount when females are not in a receptive position; most such mountings seem to be unsuccessful.

Discussion of the Repertoires

Messages and Functions

Although observations are as yet incomplete, I believe that all the species probably encode, in their displays, messages about (a) interference with a tendency to locomote, (b) anxiety over potentially disruptive situations, (c) aggressiveness, usually with some indication of defensiveness or offensiveness, and also of relative inhibition, (d) possibly fear, and (e) identification in terms of species, individual, and sometimes sex and breeding condition. The signals encoding these messages occur in a great variety of situations, and often appear to overlap in function in the usage of each species.

It is possible, although far from proven, that even in different species different messages may in some cases be employed for the same function. For instance, the CdVs of most species probably have at least the function of repelling neighboring males and thus must share some meaning(s) in common, but their messages appear likely to be somewhat different from species to species. In some species they are relatively poorly differentiated in form from the LHVs with which they intergrade regularly; in other species they may incorporate a message more closely related to that of the CV, as they resemble it in form. Employed in similar "immediate" contexts they must still differ in "historical" contexts, since they operate with respect to the genetic instructions peculiar to each species. Possibly the similarities of form between CdVs and other vocalizations in different species are in each case indicative of an absence of much need to distinguish the vocalizations from each other. For example, it may not be important in *T. vociferans* for the LHV and CdV to be easily distinguished, while it may be important in *T. tyrannus.*

Sexual Differences in Repertoires

Females of all species display much less than males. This is partly because of the difference between the roles of the sexes; females, for instance, do not patrol, rarely guard, do not engage in countercalling or Tumble Flights, and in the predawn twilight they apparently do not use the RRV. Even in activities which may be performed by either sex, however, females are likely to be less demonstrative; e.g., a female driving an intruding bird away from the nest often just attacks, or attacks with Bill Snaps only. Females also display less than males when exchanging greetings with their mates — their LHVs are almost always briefer than the male's, as is the accompanying WFt. The female LHV is also more variable than that used by males, and this variation is extreme in *T. forficatus.* The most extended display of females is the CV that most species may use in the nest, or when nest site prospecting. This may not only be quite extended, it is usually given at times when an attendant male is silent.

Why males display more than females is not clear, but possibly it is because their behavior is more likely to change rapidly, and is thus less predictable without added information. Female behavior may be sufficiently constant to permit relatively long term predictability, while males may need to display to allow even short term predictability, at least at times when their moods are rapidly changing. When using an extensive CV a female may be indicating that her behavior has become relatively unpredictable. At other times, a nest-building female is likely to continue to work on her nest, and an incubating female to continue incubating, all with lapses occasionally for foraging, a non-social activity. The mates of such birds, on the other hand, may forage or guard relatively placidly, while fairly quiet, or may become aroused perhaps by repeated intrusions of some potential rival or predator. Often aroused males begin to behave erratically to the extent that they may attack all manner of birds including their own mates, or may go to some far part of the territory for an encounter or for patrolling; at such times they display frequently.

Vocal vs. Non-vocal Display

While relatively little attention has been devoted to the detailed observation of visible displays, it seems that these vary relatively little among the species. Most seem to overlap considerably in message with some of the vocalizations, but their partially redundant information is supplied to different sensory receptors of the recipient animal. The use of the visual sensory systems in itself enables the imparting of additional information, since the orientation of a bird in the Crouch, for instance, provides a form of pointing, of indicating the opponent, which is not available to the vocalizations accompanying the Crouch. In some cases a gestural display may have a narrower range of usage than the vocalization which accompanies it, and may help to distinguish between two closely similar vocalizations (e.g., in *T. vociferans* usually only the LHV and not the CdV is accompanied by a WFt, or, in any event, if there is a WFt the communicator is experiencing some form of locomotory hesitance).

With the exception of the Tumble Flight, most non-vocal displays are used primarily in encounters when the participants are close to one another. Such displays are, in fact, efficient only at short range while sound signals are much more practical for long range communication. At the same time, sounds have a number of advantages (see Thorpe, 1961, p. 9) even at short range and so may carry the bulk of the communication load.

Form of Vocalizations

The vocal repertoires found within the genus comprise some very simple calls, some series of simple elements, calls which combine dissimilar elements, and other calls which are series of complex units, the units comprising unlike elements. Most of the recognizably different vocalizations within each species are spanned by infrequently or commonly used intermediates. Where the functions of different vocalizations (i.e., the effects of responses by recipients, the effects of meanings) need be different, the vocalizations should be easily distinguishable (as are, for instance, the RV and ILHV of *T. tyrannus*). Where the message encoded is relatively complex (as it may be in this ILHV), it may best be encoded in a relatively complex signal which will permit some variation to encode relative shifts in the component aspects of the message. Moynihan (1964) has pointed out that complex signals are probably relatively easy to misunderstand, and that it often appears to be better for them to be structured not of a blend of different elements, but of a juxtaposition of unlike forms. Thus the ILHV of *T. tyrannus* may be structured of a component encoding a relatively aggressive state, followed by a contrasting component encoding a more hesitant or even fearful state, and some variation in the relative durations of each component is possible.

Vocalizations comprising a single combination of two unlike elements do not appear to be common in *Tyrannus*, and thus far are known only in the ILHVs of *T. tyrannus* and *T. verticalis*, and the RHV of *T. vociferans*. A combination of like and unlike elements or units in series is more common, though, and characteristic of all of the RRVs. The prolonged LHV forms of almost every species are also of this sort. (*T. savana* is probably an exception and *T. albogularis* may be another; in *T. couchii* the initial "tzheeer" differs from the units of the series in the male LHV, but is not always present.)

The CdV of most of the same species also comprises combinations of unlike parts, with *T. couchii* again not strictly comparable since its CdV is usually simple but apparently may combine with a series of ILHVs. In most cases it is difficult to compare the repertoire of *T. dominicensis* (and *T. caudifasciatus*, so far as it is known) with the others, since every call except the CV comprises a combination of a series of brief elements with one or more relatively prolonged elements. The one vocalization which comprises a series of units and which, despite its high variability in some species, almost never includes patterned combinations of contrasting elements is the CV, and it has a simple message. It is possible that the CV of *T. vociferans* is exceptional, but it is also apparently a rare vocalization, and is at present poorly understood.

Continuous variation in the form of a vocalization (or other display) is a different matter from the juxtaposition of unlike forms. Continuous variation undoubtedly modifies the basic message of a signal, but, to the extent that it makes different signals more similar, it must also increase the possibility that two signals will be confused by the recipient.

The most common form of continuous variation in *T. tyrannus* and in at least some of the other species entails the addition of increasing degrees of harshness. As I mentioned in an earlier chapter, vocalizations can be made more and more harsh until they lose their basic forms and become essentially indistinguishable. Thus, in *T. tyrannus* it is difficult or impossible to distinguish the harshest forms of the ILHV, RV, CV, CdV, and LHV. It seems quite probable that the message of offensive aggressiveness has become paramount by the time harshness has increased to this stage, and the vestiges of form of the different vocalizations only indicate the mood from which the communicator became so aggressive — a matter of little importance in most cases.

Continuous variation in some other cases, not involving an increase in harshness (as between LHV and CdV in some species, or between WFt and WFk) may be difficult for the recipient to "read" in the sense of obtaining an exact impression of the point along the continuum of possible forms which is being expressed. On the other hand, it may be an efficient way of encoding in one signal the messages of both displays, when both messages are relevant. Its efficiency is likely bought at the price of exchanging speed for accuracy, however, as Moynihan (1964) pointed out. Finally, repeating a display, and increasing or decreasing the rate of its repetition, is another kind of continuous variation, although it is a variation of signalling rather than of the signal. In some cases, however, as when a brief RV is repeated rapidly by a *T. tyrannus* and comes to be indistinguishable from a harsh CV, rate of repetition can also make two displays become alike.

The two species of the subgenus Muscivora both have repertoires with marked peculiarities of form. *T. forficatus* apparently lacks an ILHV and a CdV, and has a remarkably variable CV; in females of this species the whole repertoire of vocalizations seems to be highly variable and may comprise a completely continuous set of relatively common intergradations. In *T. savana* all of the vocalizations except a harsh AtV are reduced to click-like sounds, and seem to be used relatively rarely. Because of the open country they inhabit it may be that the latter, and perhaps both, species live in a relatively depauperate "sound environment" (see Marler, 1960) and have relatively few sympatric species from which their calls must be distinct. Simple sound environments lead to less elaboration of vocalizations for identifying messages and mean that signals can be simpler or more variable.

An open habitat likely has at least two more direct effects on the use and nature of the repertoires of its species, however. One is that birds living in it may be particularly exposed to predation and should make themselves less conspicuous by a minimal amount of displaying. Second, as Hudson (1892, p. 9) noted, birds of the pampas are in general relatively silent. He supposed this to be because they could see one another well, or supposed that birds of less open habitats had to vocalize more because of relatively poor visibility. In the terms I am employing signalling may be less necessary where *continuity of context* is more nearly complete. If a female on the nest can watch her mate continuously as he forages and patrols, she can know whether he has had a fight or encounter which may make his behavior relatively unpredictable for some time following, even if he does not signal about it. An instance of a female Scissor-tail watching from the nest as her male chased a rival from the territory is reported in Bent, 1942, p. 87. Similarly, neighboring males can each know when the other is patrolling by seeing him patrol, and have less need to hear him proclaim. Predictability increases as the chances to observe a bird continually increase, as more recent historical context becomes available. There are limits to this, of course, and these are well illustrated by the common usage of LHVs in greetings between mates at least early in the season. When one individual approaches another closely there is likely considerable opportunity for a misunderstanding even where continuity of context is nearly complete.

The repertoires of *T. dominicensis* and *T. melancholicus* (and possibly others, including at least *T. albogularis* and *T. caudifasciatus*) include vocalizations which, at least to my ear, are relatively difficult to tell apart. This may be much less of a problem for the birds, but if not it will require an explanation. The environment may again be relevant, although in a different way. Within most of the range of *T. melancholicus* and probably of *T. dominicensis*, the length of the breeding season may be relatively great. Where seasonal change is not rapid there may be no great pressure to settle social problems quickly, and a less efficient set of displays may do well enough.

If some selection pressure exists which would act to counter increased distinctiveness of the displays within a repertoire, then the acceptable level of efficiency might permit an evolutionary compromise. The myriad of other avian species among which these particular kingbirds live creates a very complex sound environment within which each species must be able to distinguish the vocalizations of its conspecifics, i.e., there is a second sort of distinctiveness as a strong requirement for the displays. There is probably a variety of ways for coping with this problem, some leading to elaboration of repertoires, and others to simplification. By having all vocalizations within a repertoire share a common set of characteristics a species may obtain displays all of which differ from the displays of sympatric species in the same ways. Such displays would be easy for a member of the species to recognize as "pertinent to read" although they would be less easily distinguished within that species' repertoire.

FIGURE

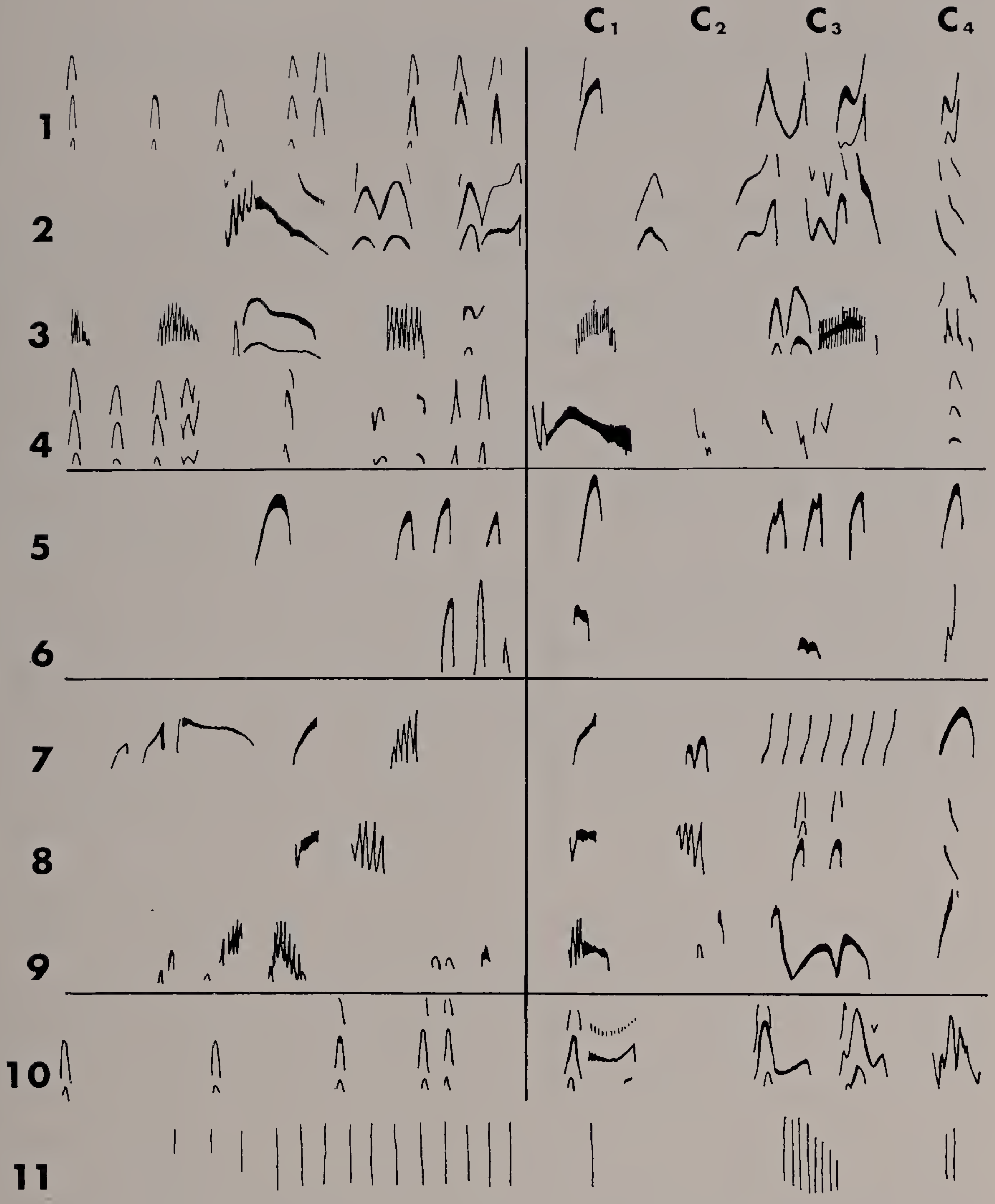


FIGURE 9:1. Diagrammatic comparison of the RRVs of the species for which this vocalization is known. The species are as follows: (1) *T. verticalis,* (2) *T. couchii,* (3) *T. vociferans,* (4) *T. crassirostris,* (5) *T. melancholicus,* (6) *T. niveigularis* (not necessarily the RRV, but a call recorded in a flight display), (7) *T. dominicensis,* (8) *T. caudifasciatus,* (9) *T. tyrannus,* (10) *T. forficatus,* and (11) *T. savana.*

The vertical line separates what I have called the complex portions of the RRVs from the preceding portions. These terminal "complex" parts have been subdivided (C_1, C_2, C_3, C_4) into an initial, usually prolonged, element, subsequent brief elements, a region in which frequency variation is usually most extreme, and a final, brief ending.

Chapter 10.

ECOLOGY AND ZOOGEOGRAPHY OF THE GENUS *TYRANNUS*

Habitats

Members of the genus *Tyrannus* do not frequent either dense forest or completely open country, although they may occasionally be found in either, but one species or another does inhabit almost any sort of intermediate vegetation. Some are found on the edges of dense forests and in many kinds of openings whether due to fire, clearing by man, water-soaked soil, or the presence of a river bank or lake shore; they also occur among the trees of sparse forests. Some species inhabit quite arid regions, and seem to require only a supply of some sort of commanding perch, be it a scattering of yucca plants or the presence of fence and telephone wires.

Most of the species are tolerant of a wide range of habitats. A distinction must be made, however, between their habitat requirements for nesting and for foraging. The perches used for foraging may be found mostly in a habitat adjacent to the tree or man made structure used to support the nest; several species may nest together in one habitat and yet apparently feed in different habitats. I shall treat each species below in the order in which it appeared in the foregoing presentation of the display patterns.

Tyrannus tyrannus

The original habitat of the Eastern Kingbird in eastern, northern, and far western North America was probably forest edge of all sorts, and whatever areas of thin, irregularly broken forest (like pine barrens) and brushland that may have existed on sandy soils and elsewhere. In forested regions today it occurs along all kinds of edge and often throughout burned areas where some tall trees, dead or alive, remain standing; it shows a strong preference for marshy areas and is often abundant in flooded forests. Beaver ponds, silting lake shores, and some sorts of bogs may have been important to it before the forests began to be cleared. Where the opportunity is available it shows some preference for trees surrounded by water, or for limbs overhanging water, as nest sites. In the most detailed example of which I am aware, one half of 70 nests of *T. tyrannus* found by Davis (1955) by Flathead Lake, Montana, were over water. Further, flooded areas have many dead trees, and if these offer large open cavities it evidently prefers to nest in them rather than in the open. Today it is a common bird in eastern farmlands and orchards, along the edges of woodlots, and in trees around farm buildings.

In the western interior parts of its range where the country was open before the intervention of man, *T. tyrannus* has nonetheless benefited from at least some of the changes made, and can now often be found far from the nearest tree, perching on fence and telephone wires, and nesting on the poles. It occurs in a variety of brushy habitats, and, of course, along the sides of rivers and streams which have a riparian woodland fringe.

In those areas in which it occurs with *T. verticalis* there is regional variation as to which species has the wider habitat tolerance. In Montana, for instance, Hiatt (1942) found *T. tyrannus* about twice as common as *T. verticalis* and occurring across a greater range of altitudes; he also noted that in most cases *T. tyrannus* preferred open habitats where brush, not trees, dominated. *T. verticalis*, on the other hand, was usually more common where trees occurred in groves or grouped within small areas. In the mesquite plains of north central Texas, Hamilton (1962) found *T. tyrannus* only in prairie lowland riparian woodland, where it was rare, while *T. verticalis* occurred in these woodlands, in both the prairie lowlands and the mesa areas, and was also found in mesquite savannah and juniper-oak woodland.

The extent of geographical overlap between these two species has been increased recently, as *T. verticalis* has expanded its range eastward since about the turn of the century (for a partial summary of this range expansion see Bent, 1942).

The first *T. verticalis* was recorded in Manitoba in 1907, and the species had become common in the southwestern portion of the province by about 1927. The marshes of the Delta region undoubtedly supply unusually good foraging for both species, and both occur there at extraordinarily high population densities. The Delta Waterfowl Research Station is built on a low, wooded, sand ridge which separates Lake Manitoba from a very broad *Phragmites* marsh to the south. The trees on the ridge are primarily aspen, Manitoba maple, ash, and willows; south beyond the marsh the country is farmed, and there are scattered woodlots of oak, with aspen and Manitoba maple planted near farm buildings.

T. tyrannus is found on the edge of all the woods, and sparsely even in the open farming country as long as there are fence or telegraph poles for perches. It nests along the edges of woods and copses or in more open areas where there are lines of trees, scattered single trees or clumps of trees, or even on isolated poles. *T. verticalis*, however, is partial to the open habitats and usually nests about farmyards or beaches where one or a few trees stand either apart or among dead trees.

This difference between the two species is most clearly seen on the sand ridge. The research station is near one end of a row of cottages which is about two miles long. On either side of this area the ridge extends for several miles without buildings, and is infringed upon only by a little used road. The width of the ridge averages about 150 feet; in places where it is very narrow and occasionally flooded there are few or no trees, and in some other areas the trees have been destroyed by fire. The relatively treeless areas, including the region of cottages, are favored by *T. verticalis,* whereas *T. tyrannus* occurs throughout. Where both species occur together, their nests often alternate along the ridge.

Censuses were taken in late June over a 1.2 mile strip within the cottage area, and a 2.2 mile strip to the east. I counted, three times for each strip, the number of individuals giving the RRV in the predawn twilight. Scores kept at 0.2 mile intervals were consistent for the type of habitat represented and revealed that there were approximately 25 pairs of *T. tyrannus* per mile among the cottages, and 15.5 per mile in the other area, a difference which may reflect largely the greater width of the ridge in the former area. *T. verticalis* was much less uniformly distributed, but averaged about nine pairs per mile among the cottages, and 3.6 pairs per mile in the unsettled area. Five of the eight pairs in this last area were in a 0.6 mile strip of burned, dead trees.

Tyrannus verticalis

This species ranges widely through the interior and southwest part of the continent in relatively open, grassland country where there are perches and nest sites. For the most part it seems to require some trees, and its recent range expansion has probably been much influenced by the plantings settlers made on the plains (see, e.g., Nice, 1924). That trees are important to it, even if not always critical in determining its presence or absence, may indicate that the species is adapted primarily to nesting in riparian woodlands, and, although it feeds in open country, its distribution has been to some extent limited by the distribution of its nesting trees.

At least some populations, however, have become totally independent of trees, and in southeastern Arizona I have studied pairs that were breeding in groves of *Yucca spp.,* miles from the nearest trees. Kennedy (1915) remarks that in one arid region the species came in and used hay derricks and telephone poles for nest sites, but preferred trees which began to grow after irrigation. That several pairs will nest in a single, small grove, or rarely even in one tree (see Bent, 1942) also suggests a marked dependence on trees as nest sites if suitable foraging habitat is to be exploited. My observations at Delta indicate that in habitat that is probably uniformly suitable for foraging, nesting was restricted to locations where trees could be found that were not contiguous to other trees, and certainly not to large blocks of trees; this, too, may be a behavioral preference carried over from adaptation to nesting in riparian growth in arid country.

In the southwestern states there is a large geographical overlap between *T. verticalis* and *T. vociferans*. My observations made in southeastern and south central Arizona in the spring and early summer of 1962 indicate that the greater proportions of the populations of each species are likely spatially separated in different habitats, but no large scale censuses were made. Work done by Hespenheide (1964) in the same summer was (for the species *T. vociferans*) concentrated primarily on individuals that were in or near zones where both species meet, and, while it supports the above impression, I believe the distinction is more pronounced than his sample shows. In personal communication, Hespenheide has agreed that the distinction is more pronounced, and has cautioned that his Table 4, p. 276, should not be read as a comparison within each species of the relative numbers of nests in each of the four habitats he lists. Because of his sampling bias toward the second and third habitats and the fact that these two are in fact relatively rare, their importance is much less than might be assumed. Most of my communication studies were made on the same individuals he studied, and we noted that in nests found in regions of overlap, the species showed no habitat differences in nest site choice — both used the available tall trees (see Hespenheide's paper for data and details of habitat).

An insufficient number of observations was made on foraging habitats, but my notes indicate that *T. vociferans* spent most of its foraging time in the pine, oak, juniper associations on the sides of the canyon, while *T. verticalis* was partial to much more open desert shrub and grass areas, and foraged very little along the sides of the canyons; on the plains it was most abundant where there was a good growth of mesquite. Both species did some foraging around and over the riparian growth. *T. verticalis* did not occur up-canyon beyond areas of open grassland, and very few pairs of *T. vociferans* were found in the open country below the canyons and their riparian growth, although both species were found in the planted trees of towns. Along the Rio Sonoita above Nogales, Arizona, we found a pair each of *T. verticalis, T. vociferans,* and *T. crassirostris* all nesting within a short distance of one another in riparian trees, but all appeared to be foraging at least partly in different sites (see below). Again, all foraged to some extent over the riparian growth, but *T. verticalis* overlapped with *T. crassirostris* only on the open hillsides with good grass cover, and not on the more arid ones; *T. vociferans* was not seen foraging on these open hillsides.

Time was insufficient to make careful studies of foraging behavior at this site, and my observations were confined largely to communicating behavior; more detailed work will be necessary to determine whether or not there are substantial distinctions in the foraging habitats of the three species in their small area of geographical overlap.

From this site southward a short distance into northwestern Mexico there is a very small geographical overlap between the breeding ranges of *T. verticalis* and *T. melancholicus.* We did not see enough of the latter species in that region to know what its habitat requirements are, other than that it is dependent upon riparian vegetation, and did not see the two species together at any one site.

T. verticalis and *T. forficatus* also overlap geographically in roughly the western half of the range of the latter. I have never studied the two species at any one site, but they do occupy some of the same habitats according to Hamilton (1962), who found both in mesquite savannah and juniper-oak woodland. He found only *T. verticalis* in riparian woodlands (perhaps reflecting only the nesting preferences of the two species) however, and only *T. forficatus* in the rather xeric juniper savannah. The smaller size of the latter species likely indicates that it has different trophic requirements, and the foraging methods of the two species differ (see below).

Tyrannus vociferans

In the Chiricahua Mountains of Arizona the greatest numbers of this species occur in the lower parts of the canyons. Where there is a good cover of pine, juniper, and oak on the hillsides the bird may occur at elevations above the typical riparian sycamore trees, and where there is a good growth of oak below the canyons (as in a case we noted in the Santa Rita Mountains, and as Pough, 1957, p. 172, describes for southwestern California) a few pairs may occur out on the plains. Rarely, a pair will nest far out on the plains, having as little as one tall tree and some lesser perches; Hespenheide (1964) has pointed out the importance of having a tall tree for a nest site. Except in such cases, the foraging habitat seems to be largely the pine, oak, juniper hillsides. In exceptional cases, e.g., the townsite of Portal at the mouth of Cave Creek Canyon in the Chiricahuas where tall trees have been planted in patterns suitable for the nesting of an unusually large number of pairs, there may be considerable overlap in habitat between this species and *T. verticalis.*

The habitat preference of *T. vociferans* in southern Arizona is probably typical of much of the population, but there are other possibilities. On 13 August, 1964, my wife and I encountered a family of this species (fledglings still partially dependent and begging) in an extensive, fairly dense, sub-desert forest of *Yucca filifera* about 41 miles north of Matehuela along Mexican highway 57 in the state of Nuevo Leon. The larger, dark-leaved yuccas were up to about 30 feet in height and averaged about 60 feet apart over an understory of shrubs and *Opuntia spp.*, which was fairly dense although easy to walk through (rather like a juniper-oak hillside in the Chiricahuas). We had not found the species a few miles farther south in a denser mesquite shrubland with bushes about 15 feet tall, nor in more open *Yucca spp.* (not *filifera*) associations in the region. In the Peloncillo

Mountains of New Mexico in 1962 I found *T. verticalis* in associations of *Yucca spp.* and various shrubs which were both less dense than at the 1964 site and lacked the tall *Yucca filifera*; no *T. vociferans* were with the *T. verticalis* in 1962. Apparently the Mexican *Yucca filifera* site was suitable because it had a sufficiently dense understory and sufficiently tall plants, even though the latter were not broad leaved trees but yuccas.

On the edge of the townsite of Imuris in Sonora, Mexico, we located two pair of *T. vociferans* and one pair of *T. melancholicus* perching in willows where the Rio Magdalena winds through a grassy, flat pasture. Neither *T. verticalis* nor *T. crassirostris* was present at this site. The geographical ranges of *T. vociferans* and *T. melancholicus* are largely non-overlapping, but meet in the valleys of western Mexico along the length of *vociferans'* range. *T. melancholicus* is confined to lower elevations in this part of Mexico and so occupies on the whole a much lusher and more "tropical" vegetation than does *T. vociferans,* which is in the higher country.

Tyrannus crassirostris

I have seen *T. crassirostris* at only three sites. The first was in southern Arizona along the Rio Sonoita about 15 miles north of Nogales. The river bed is well wooded there, with much cottonwood, a few sycamores, and many densely leaved lesser trees and large bushes including a great many willows. The hillsides are steep and arid, one having a good deal of grass and some scattered shrubs, and others having about 50 per cent of the surface area exposed as bare, crumbling, sedimentary rock (most of which is nearly white, some pale reddish), and a little volcanic ash. These slopes are sparsely vegetated with *Opuntia spp.*, ocotillo, dry brown grasses, scattered woody bushes, and some sotol. The Thick-billed Kingbird was seen foraging on a variety of hillsides and over the riparian woodland, but spent the majority of its time on the most arid slopes. It perched almost solely on the dead stubs of the taller bushes; these were quite scattered as most of the bushes reached only about five feet in height. It sought the tallest, which were closer to ten feet. The cases of foraging over the riparian vegetation occurred in the evening when the arid slopes were in shadow.

In Sonora, Mexico, we located a single individual along the Rio Magdalena about 8 miles below the town of Imuris, near Terrenate. Here a nearly continous growth of 30-foot willows lined the river banks, and there were a few slightly taller cottonwoods. On one side of the river a narrow flat had been irrigated and planted in field crops and plum orchards, but the slopes of the valley were steep and arid, showing much open soil amid sparse grass and organ-pipe cacti. While we watched this bird, it foraged only by fishing in the stream (see below). Finally, a third *T. crassirostris* was observed briefly in Guadalupe Canyon in extreme southeastern Arizona, about a mile above the Mexican border. This is also an arid-sided canyon with tall trees along its river, which was then dry; about 60 per cent of the slopes are unvegetated, pale brownish and reddish rock. *T. verticalis* and *T. vociferans* also occur in the canyon, but no observations of foraging were made for any of the three species.

At all three sites the habitat feature which may have been significant was the presence of very arid, partially vegetated slopes with much open ground, sparse grass, and some cacti and bushes. In the first case, these slopes were the preferred foraging habitat of the Thick-billed Kingbird while we watched, and the more vegetated slopes and the rich riparian area were apparently favored by the other species. This observation is supported by Selander and Giller (1959) who found that in the Barranca de Oblatos, Jalisco, Mexico, pairs of *T. crassirostris* were moderately common in large trees in the "savanna" of the slopes but *less* numerous in the riparian formations — even in the absence of most other kingbirds (*T. melancholicus* was present but not common, and was found near the river). Two observations of Marshall (1957) in Sonora appear to be different, however, in that he saw *T. vociferans* feed over fields and "desert slopes" while *T. crassirostris* in the same area remained in the riparian sycamore groves.

Tyrannus couchii

In the lower Rio Grande valley of Texas, *T. couchii* inhabits the rich thorn scrub and forest which Clover (1937) calls "monte del rio." In a preserved remnant of this forest, Santa Ana National Wildlife Refuge in Hidalgo County, *T. couchii* has a dense population and nests commonly in the taller trees, especially in Texas ebony, *Pithecolobium brevifolium.* The habitat is typified by stands and scattered individuals of this and a few other tree species, sometimes hung with *Tillandsia spp.*, dense growths of various shrub species (*Acacia spp., Parkinsonia aculeata*, and others, mostly thorny), and some vines, interspersed with small grassy sites and cacti of several species, predominantly broad, four to six foot tall clumps of *Opuntia Engelmannii.* The Refuge is a patchwork of different densities of this vegetation, the shrubs varying from dense thickets to non-contiguous individuals growing amid grass within quite short distances. Most of our studies were made in this Refuge, and we made a preliminary attempt to determine which parts of the vegetation were most suited to the kingbirds. On the mornings of 18 and 19 May we counted the number of *couchii* males (13) giving the RRV in the predawn twilight along 1.6 miles of road in the western part of the Refuge. We also counted the number of *Myiarchus tyrannulus* (12) giving their RRV in the same stretch, as this was the only other large tyrannid which might in some way compete ecologically with *T. couchii.* (*T. forficatus* was present in the region, but only in much more open habitats, and we encountered relatively few of the *T. couchii* there.)

I then paced off an average of 17 equal intervals (range 16 to 19) per 0.1 mile along one side of the road and estimated the height of the nearest tree, the height of the tallest tree directly behind it (within 50 feet) and the distance of that tallest tree from the road. These data have been plotted in a number of ways. The most useful seems to be a plot of the distance from the road to the first tree 25 feet or taller, a form which gives a rough measure of the height and uniformity of the forest. Three main regions show up in this graph; in the first 0.4 miles there are 10 intervals in which a 25-foot or taller tree is within 25 feet of the road, in the next 0.5 miles there are only 4 such intervals, and in the last 0.7 miles there are 22. The distribution of calling *T. couchii* has a positive correlation with these regions (5, 2, and 6 birds) although the third region may have been more than optimally dense habitat. The distribution of *M. tyrannulus* tends slightly toward a negative correlation (3, 5, and 4 birds). Thus, within this small habitat sample, *T. couchii* seems more dependent on the number of relatively tall trees present than does *M. tyrannulus.* The foraging habits of the two species correlate well with this preference: *T. couchii,* as most other kingbirds, perches atop trees, usually on dead twigs or dead upper limbs, and pursues aerial prey, usually at treetop level or higher, sometimes in long, ascending flights. *M. tyrannulus* perches at various heights, and spends more time flight gleaning from the foliage or flycatching among the trees and lower vegetation. However, while they do help to distinguish between the two species, the data are too rough to enable a more thorough description of the habitat of *T. couchii* in this Refuge.

Such a description should someday be made, as it would be of interest to know if this species differs in habitat preferences from *T. melancholicus,* farther south in eastern Mexico. In August of 1964 my wife and I found *T. couchii* in dense thorn scrub, which was similar to but slightly more arid than the Texas habitat, in rolling country south into Mexico along the highway from Matamoros. In the vicinity of Antiguo Morelos, however, it was found in thorny but much less xerophytic scrub. West of the city of Veracruz the birds we found (see Chapter 5) were in a similar pastured thorn scrub, while north of that city the one bird we located was in a more lush second growth in an agricultural region.

Whatever the current habitat of *T. couchii,* it seems certain that it has changed either in extent or in form (or, probably, in both) since the Spanish settlement in Mexico. According to Shelford (1963) grazing and overgrazing has resulted in a spread of bushes into a region that about 1600 A.D. was a much more open grassland. If the thorn scrub is the typical habitat of *T. couchii*, then the species' range may have been even more restricted in the past than it is now. Further, it could have been limited in the south by a belt of "tropical deciduous forest" extending inland from the coast into the mountains in northern Veracruz; if the Veracruz populations of *T. melancholicus* didn't extend through that forest (they don't extend that far north today), then the two populations would have been wholly allopatric.

Tyrannus melancholicus

The Tropical Kingbird is almost as eclectic in its habitat preferences as is the Eastern Kingbird, and is even more widespread geographically. While avoiding densely forested areas it nonetheless inhabits all manner of forest edge from clearings to river banks, and is abundant where the forest has been partially removed, living along the edges of cultivated fields, in bushy hillsides and pastures, and in thin second growth woodlands. In many places its range has undoubtedly been increased by man's activities. It avoids completely treeless regions, but extends into arid country along riparian forests, and inhabits savannas and thorn forests.

T. melancholicus is sympatric in the breeding season with a number of different congeners in different places, including *T. verticalis, T. vociferans, T. crassirostris, T. albogularis, T. niveigularis, T. dominicensis,* and *T. savana;* and some of its populations overlap with *T. tyrannus* and *T. forficatus* in the winter. The cases of overlap in the breeding season are in most cases limited in area, and are discussed under each of the respective other species; the data suggests that for the most part there is probably a difference in foraging habitats. Whether or not there is competion for food resources among wintering populations is not clear from the few data available, but it seems possible.

T. melancholicus cannot be characterized as a bird of thorn-forest, as *T. couchii* may be, but in some regions it does breed in similar habitats. The only one in which I have seen it which appeared to be closely similar to the Texas "monte del rio" was a rich, dry thorn forest in southern Tucumán, Argentina, where I was able to camp briefly with Douglas Lancaster in November, 1962. The thorn scrub of central Veracruz where my wife and I found the birds, which may have been hybrids, was much more open and more influenced by cattle grazing. According to Lowery and Dalquest (1951) the Tropical Kingbird in Veracruz is found only in the relatively arid portions of the coastal plain; apparently the species' habitat preference at the northeastern limit of its range is less broad than elsewhere.

Tyrannus niveigularis

I have seen this species only in the Guayaquil region of lowland Ecuador where it inhabits seasonally wet agricultural and second growth countryside. If its habitat is distinguishable from that of *T. melancholicus* in this region, it was not immediately apparent. Marchant (1959) has worked in the more arid coastal country of the Santa Elena peninsula of Ecuador where *T. niveigularis* enters and breeds in the wet season, but does not remain through the dry season. In that region *T. melancholicus* does not occur, suggesting that some habitat distinction between the two species does exist for at least part of the population.

Tyrannus albogularis

Helmut Sick (personal comm.) has described the habitat of this species as being "Cerrado, Capão (=little dry forest isolated in the Cerrado), riversides in the Cerrado region." Cerrado is a rather broad term referring to much of the seasonally arid, semi-open country of the Brazilian interior, and includes primarily wooded savannah (see Aubréville, 1961) with some moderately dense thorn scrub in places. My own observations fall within his generalization, and also serve to indicate the possibility of some habitat separation between this species and *T. melancholicus.*

The single individual which I saw in the Territory of Amapa was at the damp edge of a copse (locally, an "*ilha de mata*") in savannah of the sort found in various coastal regions of the Guianas. It was perching in fan leafed *Mauritia* palms and in bushes. A few miles away, where the savannah met the edge of the continuous forest, were scattered *T. melancholicus*, but they did not appear to come out from the forest to the *ilhas.*

The families of *T. albogularis* seen in the interior of Sao Paulo and Minas Gerais were not in cerrado but in large marshes in a cattle grazed countryside. These marshes were composed primarily of bunches of a tall (up to 10 feet) grass, identified for me by Helio Camargo as *Paspalum intermedium,* amid which were scattered bushes (Rubiaceae). Where surface water was present in the center of the marshes the bunches of grass were sparser, and an emergent blue flower, *Eichlornia sp.*, was abundant.

The outer, drier parts of the marshes had scattered *Mauritia* palms and fewer bushes; between the clumps of tall grass was a mixture of lower grasses. Beyond this was open, grazed cerrado with scattered bushes and patches of second growth scrub, and on one side of the larger marsh was the north bank of the Rio Grande — a low, muddy ridge, about 30 metres wide and lined with trees.

It was in the outer parts of the marshes that we found *T. albogularis,* perching on the palms and bushes and feeding over the grasses.

Families of *T. savana* were abundant and feeding widely over the marsh. *T. melancholicus* was also present, but not in the marsh. It was found at places in the surrounding countryside and in the strip of trees along the bank (really a natural levee) of the river. It fed over these trees and over the river, but I did not see it feed over the marsh. *T. albogularis* fed over the marsh and its edge, and over the inner edge of the line of trees where it met *T. melancholicus*, but it did not, in the brief time I could watch, approach the river side of the trees or venture out over the drier countryside.

I doubt that the separation of the two species' foraging areas is as clear cut as this small sample seems to indicate, but I do suspect that a degree of habitat distinction will be found. At the moment it is difficult to see the nature of the distinction, but it may be that *T. albogularis* will accept a habitat which is brushier, or which has fewer or more widely spaced commanding perches than will *T. melancholicus.*

Tyrannus dominicensis and *Tyrannus caudifasciatus*

At least in Jamaica these two species overlap considerably in various habitats, but each shows some preference. On the whole, *T. dominicensis* is more likely to be found where there are scattered tall trees and grass or at least relatively low vegetation. *T. caudifasciatus* is more likely to be seen in and on the edge of good secondary forest, and on the edge of tall forest. Both are relatively rare in thorn scrub, especially in the more xeric forms. Some *T. dominicensis* live in the coastal mangroves and in other coastal vegetation, especially if there are tall palms along the beaches.

T. dominicensis does occur in and on the edge of forested areas, particularly, I think, if there are riparian stands of tall trees cutting through scrubby, broken, second growth. *T. caudifasciatus* also occurs in brushy fields away from dense stands of trees, but in my experience relatively rarely. I think it ranges somewhat higher, on the average, into the mountains than does *T. dominicensis*; this may be related to the greater amount of forest there. Dr. and Mrs. A. S. Rand spent the year of 1961-62 on the island, and tell me that *T. caudifasciatus* was more common at lower elevations in the winter when the migrant *T. dominicensis* was not present.

The habitat preferences were also obvious in artificial habitats, such as the landscaped parks of the University of the West Indies campus and the Hope Botanical Garden. Here *T. caudifasciatus* was largely restricted to copse-like denser plantings, while *T. dominicensis* ranged into or over these but spent most of its time among the more scattered trees. Such parks, in fact, seem to be a better habitat than any natural one I've seen, and population densities of at least *T. dominicensis* are unusually high in them.

In other man made habitats such as residential areas, pastures, and borders of cultivated fields, *T. dominicensis* is usually fairly common, and usually substantially more common than *T. caudifasciatus*. I might add that, while my estimate of the habitat preferences of these species is based on field work done solely in the month of April, R. E. Ricklefs kindly did a wide-ranging survey for me while working on Jamaica in August, 1965, and found an apparently identical pattern.

Finally, the distribution of nests may also reflect the habitat preferences. All four nests I found of *T. caudifasciatus* were built in trees each contiguous with several other trees in or on the edge of moderately dense stands. The two nests of *T. dominicensis* which were being built when I left Jamaica were both in isolated palm trees.

The same habitat preferences apparently hold on Cuba (Rutten, 1934). Similarly, Wetmore and Swales (1931) report that *T. dominicensis* on Hispaniola is found in towns and villages, and in mangroves, and is common "about fields and pastures but not . . . the forests." *T. caudifasciatus* they found less common, and stated that it replaced the former species "in areas of forest" being found "almost entirely amid heavy growths of trees" and in coffee plantations. Bond (1961) describes the habitat of *T. caudifasciatus* for all of its range, and says that it is "more of a woodland species than the Grey Kingbird, but often seen in rather open country." Both Bond and I have found *T. caudifasciatus* in open country at sites where *T. dominicensis* was not present.

In the United States, *T. dominicensis* is apparently restricted to coastal habitats including citrus groves and the trees of towns and cities along the coast, while *T. tyrannus* breeds in the interior (Bent, 1942, Brodkorb, 1950, and Sprunt, 1954). In southern Florida its habitat is primarily mangroves, but in northwestern Florida it is almost confined to a "dense jungle of saw palmetto, vines, scrubby live oak and stunted magnolia," a pale-colored vegetational association on the leeward side of the Gulf Coast sand dunes (Bent, 1942). Bent also mentions that in the Bahamas it also nests in pines.

In South America I have seen *T. dominicensis* only briefly in coastal British Guiana, where it occurred in Georgetown (abundantly in the botanical gardens) and local villages, in trees along drainage canals, and at the edges of woods. There is little detailed description of its habitats elsewhere in northeastern South America, but these do not seem to differ from what I observed. Friedmann and Smith (1950) have remarked that in December in Venezuela the individuals they found were "usually together with *Tyrannus melancholicus chloronotus;*" it would perhaps be worthwhile to investigate the ecology of this association.

Tyrannus cubensis

Bond (1961) gives the habitat of *T. cubensis* as "woodlands, in particular pine forest. Also wooded borders of swamps." Apparently it overlaps in habitat with *T. caudifasciatus,* which also breeds on Cuba and the Isle of Pines. The species is relatively rare, perhaps because of man's destruction of its habitat in much of Cuba. Rutten (1934) found it only in the remnants of the formerly vast "high pine woods" of Pinar del Rio province. To Barbour (1943) it was characteristic primarily of deep lowland woods, and he pointed out that these habitats have been the most rapidly destroyed.

Tyrannus forficatus

The Scissor-tailed Flycatcher is an inhabitant of grassy, open prairies where there are scattered bushes, usually mesquite or juniper, or a riparian woodland of some sort providing convenient perches. Today fence wires and telephone wires are also used for perching, and the poles for nesting (sometimes even when trees are available). Planted trees around farmhouses or towns are also used. Where they overlap with the ranges of other kingbird species (*T. verticalis* and *T. couchii*), most individuals probably tend to be separated by their habitat preferences, the Scissor-tails taking the more open habitat. Artificial plantings around residences (used by both *T. forficatus* and *T. verticalis*) may provide the cases in which the habitats are least distinct. The spread of "lowland scrub" (Shelford, 1963) into the "*Acacia* grassland" after the introduction of cattle grazing by Spanish settlers may have forced the Scissor-tail out of most of the northeastern corner of Mexico while permitting *T. couchii* to expand there.

In winter *T. forficatus* may overlap considerably with the northernmost populations of *T. savana,* and could conceivably be one of the reasons why the latter is rare north of Panama. Lowery and Dalquest (1951) report the two occurring together in Veracruz, but, interestingly, Slud (1964) reports that they are largely allopatric in Costa Rica while the Scissor-tail is wintering there.

Tyrannus savana

The habitat requirements of the Fork-tailed Flycatcher are closely similar to those of *T. forficatus.* It occurs on a variety of grasslands, from nearly treeless savannahs to sparse thorn scrub, but seems to be most common on savannah with many scattered bushes. In the state of São Paulo, Brazil, the highest population densities I saw were always in and near marshes. It may also have an opportunistic response to flooded areas; Gibson (1918) found it extraordinarily abundant in the vicinity of Buenos Aires, Argentina, when much land was flooded in the summer of 1913-14. In February, 1963, I saw enormous flocks of non-breeding *T. savana* in the vicinity of Manaus, Amazonas, Brazil (thousands roosted nightly in the city parks) and in the daytime found some of the birds scattered in smaller flocks in some of the scrubby fields which have been cleared around the city. Their lines of flight when coming in to roost, however, suggested that many of the birds might be spending the days in the flooded forests of the nearby Amazon.

In the breeding season Fork-tailed Flycatchers overlap geographically with at least *T. melancholicus* and *T. albogularis.* Their habitat is on the whole much more open than that of the former, but may not be distinct (unless *T. albogularis* requires taller perches) from that of the latter in regions of sympatry.

Foraging Behavior

Kingbirds are well known for their spectacular methods of aerial pursuit of insect prey. Typically, they perch high on an exposed branch and actively survey the air around them, launching out after passing insects that may be within a few feet or as far off as over 100 feet, sometimes climbing almost vertically above their perch, sometimes dropping to the ground. I have made some attempt to measure the air space used by Tropical Kingbirds feeding along the forested shores of Barro Colorado Island in the Canal Zone, comparing this with the air space used by a number of closely related species from other genera feeding in the same immediate vicinity.

From Fig. 10:1 it can be seen that the kingbirds take their prey from a much greater range of distances from their perches than do the two smaller flycatcher species, *Myiozetetes similis* and *Pitangus lictor.* In part, the kingbirds may have been taking larger prey, which could be seen farther, than were the *M. similis,* but they were taking on the whole smaller prey than the large-billed *P. lictor,* which at the times of the observations was specializing on Odonata. Both *M. similis* and *P. lictor* seemed to be concentrating their attention on prey relatively close at hand, while *T. melancholicus* showed no such preference.

Tables 1, 2, and 3 compare the perch heights and prey heights of the three species, and again, the Tropical Kingbird has much the greatest range, and utilizes higher perches and prey than do the other two species. I have made too few counts on the behavior of other species to obtain significant data, but my field impression is strong that other kingbirds differ from sympatric closely related flycatchers of other genera in much the same fashion. They are on the whole even more distinct from species of less closely related genera. For instance, species of *Myiarchus* (which are usually of about the same size as kingbirds, and which overlap with them in most forested regions) usually feed by perching and peering for prey, which is then taken by flight gleaning. This method is much less active than that of kingbirds, and tends to keep *Myiarchus* flycatchers within woods and under canopies, rather than out in the open where the kingbirds are.

Kingbirds are not restricted solely to aerial pursuit, however. Some-

PREY HEIGHT →

↓ PERCH HEIGHT

	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40	40-45	45-50	50-55	55-60	60-65	65-70	70-75	75+
0-5	1	1		2												
5-10	3	3	3	4		2										
10-15			2	2	1	1										
15-20	1			2		1										
20-25				1												
25-30					3	3	1	1								
30-35	1			1		1	4	4	1	4		1				
35-40	1					2	3	4	4	4		1				
40-45																
45-50										10		1				
50-55								1	1	1		1				
55-60								1		10		43	1	10		4
60-65																
65-70									1					2		
70-75																
75+																10

TABLE 1. A comparison of the heights (in feet) of flying prey taken by *T. melancholicus* foraging along the forested shore line of Barro Colorado Island. Note the great range of perch heights used, and that prey are taken on flights upward and downward about equally over most of the range.

times they flutter in front of foliage and "flight glean" (pluck prey from the leaves while fluttering) or pick small fruits. At other times they perch and take fruits, or peer about from a perch for prey items which can be gleaned within a few feet. This last form of foraging is relatively rare, as is dropping to the ground to take prey or taking prey from on or under the surface of water. There is much hourly, daily, and even seasonal variation in their foraging methods, but in general aerial pursuit and capture is the usual behavior, and flight gleaning is used most on very windy days or when an abundant food source

PREY HEIGHT

PERCH HEIGHT	0-5	5-10	10-15	15-20	20-25	25-30	30-35	35-40
0-5	19	1		1				
5-10		5	3	1				
10-15		1						
15-20				2	1			
20-25								
25-30								
30-35								2
35-40								1

TABLE 2. A similar comparison of heights (in feet) for *Myiozetetes similis.* Although the small sample of 37 observations does not permit confident generalization, the preferred perch heights are clearly much lower than for the kingbird.

is discovered. Aerial flycatching remains common even when bountiful supplies of small fruits are available and being taken.

In the subgenus *Muscivora* there is relatively less of the spectacular aerial pursuit and much more hovering close over the vegetation, with inspection of it and the air space immediately above it. I first became aware of this in the Scissor-tailed Flycatcher as I watched birds hovering into a wind over patches of spring flowers, and moving from side to side in a search pattern above the flower heads. They were spreading their long rectrices and making frequent minor movements of them, suggesting that the feathers might be important in enabling them to control their position in the unsteady wind. I have since seen skillful hovering very frequently in both species of *Muscivora*, on both calm and windy days, and believe that the long feathers may be useful in making changes of direction while hovering. Hover-

PREY HEIGHT

PERCH HEIGHT	0-5	5-10	10-15	15-20	20+
0-5	57	3			
5-10	9				
10-15					
15-20				2	
20+					1

TABLE 3. A comparison of heights (in feet) for *Pitangus lictor,* similar to Tables 1 and 2. The sample of 72 observations shows that preferred perches are very low and that prey are usually taken on level or downward flights (i.e., usually near the surface of the water). The prey were in almost all cases Odonata (sample taken over several days on two different years, at sites in Gigante Bay, Barro Colorado Island).

ing is certainly much more common in this subgenus than in the other kingbirds, and both the long outer tail feathers and the relatively small body sizes may be adaptations for it. Probably skill in hovering is important in an environment in which there are relatively few perches, and in which the insects may often fly close above the low vegetation.

Even when not hovering, the long forked tails seem to be very useful in aerial maneuvering, and I have noted that they are apparently employed (i.e., are suddenly spread or closed, or set at a new angle) when a bird suddenly checks its course, or makes an extremely sharp turn. Similar observations are reported frequently in the papers of naturalists and collectors who have commented on either species; it also seems to be true that other species with similarly forked tails, such as the Swallow-tailed Kite (*Elanoides forficatus*) are unusually maneuverable.

The fact that both Scissor- and Fork-tailed Flycatchers spend relatively more time obtaining prey on the ground than do other kingbirds is probably also related to the openness of their habitats. Several authors (e.g., Fitch, 1950, and Bent, 1942, for the former species, and Skutch, in Bent, 1942, for the latter) have commented on this habit, and I have observed it in both species. In Texas in the spring of 1964 we often saw Scissor-tails drop to the ground in Laguna Atascosa National Wildlife Refuge, and were several times able to determine that they were taking not insects but small crabs.

INTRAGENERIC COMPETITION

Most of the species of *Tyrannus* appear to be separated either by geography or foraging habitat. Most cases of overlap of habitat have been considered previously, but some require further discussion. *T. dominicensis* and *T. caudifasciatus*, for instance, are only partially distinct in habitat preferences and often occupy the same immediate area for at least part of their foraging. The latter, however, very often does not feed in the typical aerial pursuit fashion of the genus, but uses the perch, peer, and flight glean method of *Myiarchus*. Because of this it probably takes its prey largely from a different supply source than that exploited by *T. dominicensis*, although this presumably may bring it into competition with sympatric *Myiarchus spp.*

Where the ranges of these two kingbirds and *T. cubensis* overlap another problem arises, as the last is also described as a woodland species. Barbour (1943) states briefly that it hunts from the tops of tall trees and takes insects, lizards, and small birds. This makes it seem to be ecologically more of a shrike or small hawk than a kingbird, although other large flycatchers with large bills, such as *Pitangus sulphuratus, Megarynchus pitangua, Myiodynastes maculatus,* and the species of *Agriornis*, take similar prey.

Differences in bill size, to the extent that they reflect a difference in type of prey, may also be relevant in reducing competition between *T. verticalis, T. vociferans,* and *T. crassirostris,* although Hespenheide (1964) has shown that there are no geographic trends toward greater distinctiveness in this characteristic where the populations are sympatric.

Differences in body size of sympatric congeners may be important in reducing competition between species of the two subgenera, although it has already been pointed out that (a) the feeding methods of *Muscivora* probably differ both qualitatively and quantitatively from those of *Tyrannus,* and (b) the two *Muscivora* species apparently occupy habitats that are for the most part more open than any used by *Tyrannus spp.,* with the possible exception of *T. albogularis.*

I do not know to what extent there are differences in foraging habitat between *T. tyrannus* and *T. verticalis* in most regions where the two are sympatric, since the only case I studied centered around the Delta marshes, a source of unusually abundant food. Often I saw one bird of each species feeding in turn within the same swarm of insects, and I noticed no readily apparent distinction in their general foraging patterns, perhaps because I devoted almost all of my time to studying display behavior. The surprising habitat preference displayed by *T. verticalis* in selecting as a nest site trees or structures which were not contiguous with other trees resulted in some measure of separation in foraging, in that some areas were inhabited only by *T. tyrannus.* In the absence of further evidence, however, it seems quite possible that these two species may compete in parts of their ranges, and that the range expansion of *T. verticalis* may be being made at some expense to *T. tyrannus.*

Finally, it is necessary to point out that most of what I have said pertains to populations during the breeding season. Various geographical overlaps occur when populations migrate, and species of similar habitat and foraging ecologies are apparently brought together. The extent to which they do or do not compete has not been investigated.

Zoogeography

Kingbirds of the subgenus *Tyrannus* can be divided at a glance into a colorless and a colorful group. The former (excepting the color of the concealed crown patch) is white and gray, grayish brown, or black; the latter is characterized by yellow or yellowish underparts, usually a gray head, and olive-green, olive-brown, gray-green, or brownish upperparts. There is a nice correlation between a division of the species into these two groups and their geographical distributions — the colorless birds are found in the West Indies and eastern and northern North America, and the colorful ones in South, Middle, and western North America. It looks as if an eastern line has been thrown off the kingbird stock into the West Indies, and thence to eastern North America, and has, during its evolution, lost its color.

I think a second correlation, ecological rather than geographic, may suggest how the color came to be lost. There appears to be a relationship between the color and/or density of pigmentation of the dorsal plumage of each species and the color and/or brilliance of the foraging habitat, or of the foraging habitat that probably existed before human modification of the environment. This matching of back and background is evident (see below) in every species of the genus and must be the result of a strong selective force acting throughout the evolution of kingbirds. It is not hard to guess what this might be; kingbirds, because of their methods of foraging and of nest defense, spend most of their time on the most exposed perches available. They are alert, highly maneuverable birds, but they cannot be constantly aware of their entire surroundings. An individual which is preening or resting is to some degree susceptible to aerial predators, and the color and density of pigmentation of his dorsal plumage must confer an advantage to the degree that it corresponds to the color and tone of the habitat.

Of the species of the "colorful" group, the Tropical Kingbird has, on the whole, the richest, greenest habitats, and has the most colorful plumage, its subspecies in more arid regions usually being paler. *Tyrannus couchii,* which has been thought of as a pale subspecies of the Tropical Kingbird, inhabits a relatively arid, sunny habitat, with paler vegetation and exposed, pale earth. Cassin's Kingbird inhabits the darkest vegetation of any of this group (including not only the junipers, but the *Yucca filifera* groves) and has the darkest plumage. The Western Kingbird forages over grasslands and is colorful but rather pale, while the Thick-billed Kingbird forages over grasslands and arid, partially vegetated slopes and is extremely pale and nearly colorless. In fact, the near absence of color of this species, a member (geographically and by virtue of its trace of color) of the "colorful" group, is a strong point in favor of the hypothesis.

Both of the species confined to South America are paler than the brightest Tropical Kingbirds, but not so pale as the Thick-billed. This accords well with what we know of the habitat of the White-throated Kingbird, but our lack of sufficient knowledge of the principal habitat of the Snowy-throated Kingbird prevents as sure an interpretation. The Snowy-throats I saw in the Guayaquil region inhabited a semi-open, rather lush and decidely green environment which in the dry season, however, is thoroughly brown. Marchant's birds on the Santa Elena peninsula migrated in from a presumably lusher environment and bred during the verdant season of that arid region. His description of the habitat indicates that the vegetation is sparser than in the Guayaquil area. It seems likely that the pale plumage and greenish cast of the Snowy-throated Kingbird represent a compromise solution to a changing environment that is seasonally arid.

There is no reason to suppose that kingbirds originated in the West Indies, and I shall follow the compelling arguments of Bond (1963) that the West Indian populations arose after an invasion from a stock of Central American origin. Whether or not the invaders were from a relatively pale population is probably not important, but the nature of the habitats available at their Greater Antillean landfall is. Before the advent of European settlers these islands must have supported large and dense forests, and there would have been very few broad, slow rivers offering the lowland rivershore habitat used by Tropical Kingbirds today on the mainland. Some arid thorn scrub, a few savannahs, a considerable amount of fringing mangrove, and some other open coastal vegetational associations would have provided the tenable habitats. These would all have been open and sunny, the mangroves in fact glaringly bright, and characterized by relatively pale vegetation. The "founder population" was probably small and ripe for a "genetic revolution" (for the theory behind this hypothesis see Mayr, 1954) under the influence of selection by predators. I propose that the descendants of the original survivors evolved a pale plumage rather like that of present day *T. dominicensis*, and lost the genetic basis for producing the pigments of their ancestors. At some time, some of these birds invaded the edges of the forests, a more humid and darker environment. From these we have obtained *T. caudifasciatus* and *T. cubensis*; species which are darker, but not more colorful.

The one other "colorless" kingbird of the subgenus *Tyrannus, T. tyrannus,* could well be the result of an invasion of eastern North America by a West Indian stock. Its dark dorsal plumage and its habitat preferences suggest that it might be related most closely to *T. caudifasciatus.*

If we ignore the unique salmon patches of *T. forficatus*, the subgenus *Muscivora* must also be viewed as "colorless," although its geographic distribution suggests that its evolution had little to do with that of the West Indian group. As both species inhabit open, arid environments and are similarly exposed to predation by their habits, it seems quite possible that the colorlessness of this subgenus has been an independent but parallel development.

The phylogenetic picture suggested by this consideration of the geographical distribution of plumage characteristics is supported and even extended by the evidence from similarities of vocal repertoires. An attempt to round out the inferred phylogeny is presented in the next chapter.

Figure

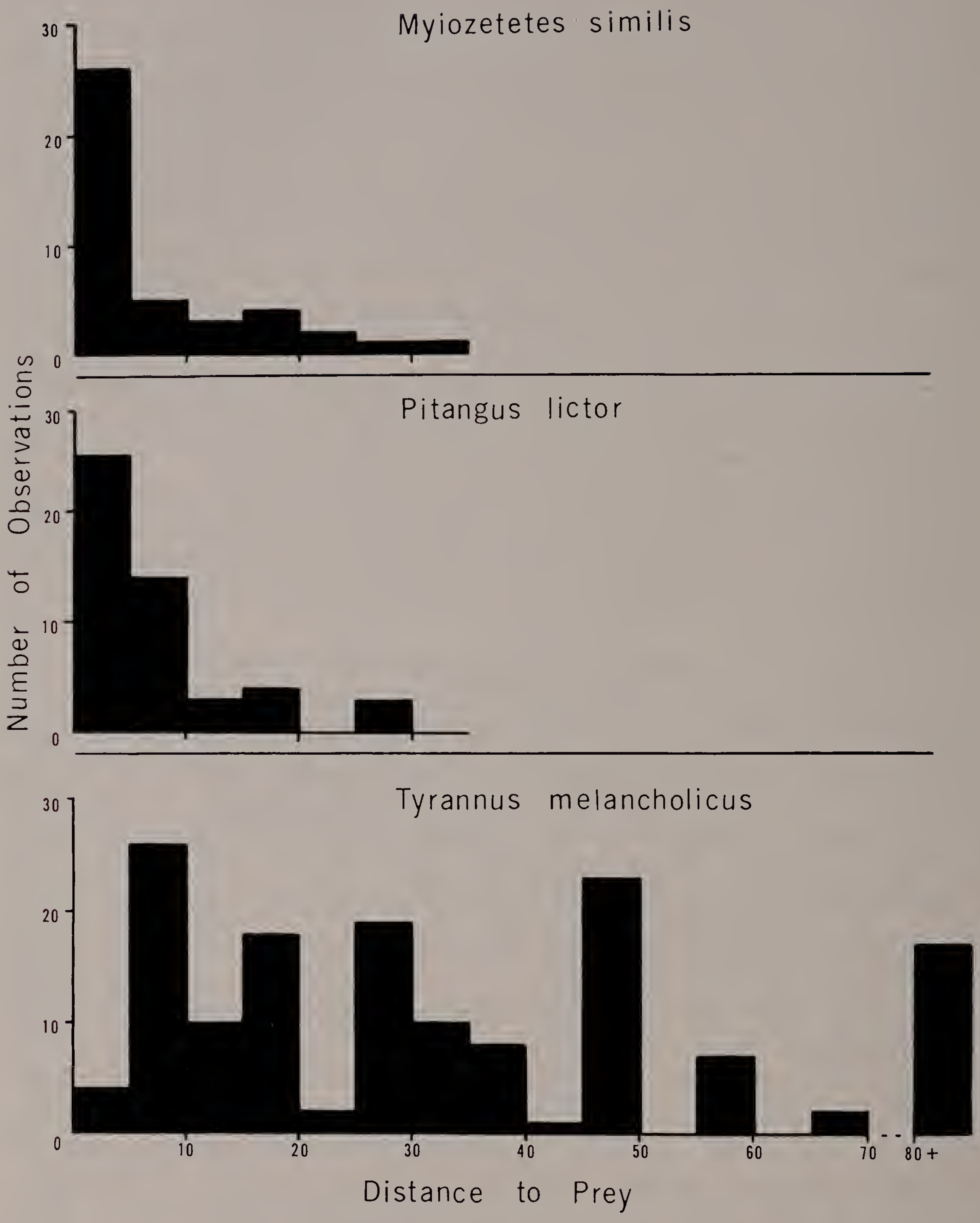


Figure 10:1. A comparison of distances (in feet) flown to capture prey by three closely related species, foraging along the forested shore line of Barro Colorado Island. Note that (a) the kingbird tends to fly much farther than the others, although (b) it does not wholly ignore the closer prey.

Chapter 11.

TAXONOMIC CONCLUSIONS

In Chapter 1 I stated that a knowledge of the patterns of communication can help us understand the history of the evolution of *Tyrannus.* No claim is made that this information alone can clarify the history, and certainly as many other features as are available must be examined before making any conclusions. As the primary contribution of the current study is information about behavior, however, I shall begin by examining what our current knowledge of their communication patterns suggests about relationships between the species.

First, we must ask to what extent does a species' repertoire of signals provide a set of independent taxonomic characters? Is the repertoire a complex that has evolved with such dependence between its units that it can be evaluated only as a single taxonomic character, or are its units at least partially independent in their evolutionary potentials? The answer seems to be that many degrees of dependence are to be expected. Sometimes we can find, for instance, examples of Darwin's useful "principle of antithesis." A Wing Fluttering display that achieves its uniqueness by revealing the undersurface of the wings almost requires that a display with a largely antonymic message should show an upper wing surface which is differently colored or marked — as Wing Flicking does. Yet neither display should have much influence on the evolution of the Revealed Crown Patch. The evolution of the RCP may have been tied with the evolution of Gaping as a display, although in this case not through the operation of antithesis but (perhaps) of mimicry. Finally, it is difficult to see how any of these postural displays would have had much influence on the form of some of the vocalizations, such as the Regularly Repeated Vocalization, although we might assume that the effects on respiratory physiology of Wing Fluttering in flight might limit some aspects of the range of forms open to the Locomotory Hesitance Vocalization. There must be numbers of interrelationships between the forms of displays, which are too subtle to be apparent at our present level of understanding; but, fortunately, a comparison of the repertoires of several species can help us detect at least relatively gross features of displays which have not evolved in the same ways in the different species.

In addition to evolution for antithesis, there is also evolution just for contrast, to make different displays distinct and unambiguous, and there are various sorts of other selection pressures related to the sound environment, and the distance over which a display need be effective. These pressures must interact in the course of evolution, and, granted different opportunities, should often reach different compromises in different populations. It is abundantly clear from the data which have been presented that the species which are most similar in any one particular vocal display are usually not the most similar in some other vocal display. In short, some degree of independence of evolution does occur, and we can best proceed by examining particular instances of interspecific comparisons.

Second, we have already encountered (Chapter 9) the problem of identifying homologous units for comparison. Within the RRV displays, it was impossible to say which elements in one species were the homologues of particular elements in another species. That different species to a large degree share a basic pattern in this display suggests that the pattern, if it is on the whole "arbitrary," may be primitive and the RRVs themselves should be homologous. The pattern is found in species with quite different habitats and different social structures (such as flocking or non-flocking, year-round or seasonal territory) and so seems to be arbitrary, at least with respect to comparisons made within the genus. On the whole, the criteria I have used in comparing vocalizations (stated in Chapter 9) have been based mostly on usage, and this is not a sure way of identifying homologies. Yet the members of this genus are by all indications a very closely related group (as, indeed, are the members of the larger set to which this and adjacent genera belong), and it is extremely unlikely that they would have evolved by convergence so intricate an adaptation as their repertoires. The repertoires as a whole must be homologous, and so, probably, must be at least the gross divisions of these repertoires.

Interpretation

Now let us return to the RRVs, because the pattern of species groupings which they suggest has already been indicated. This pattern comprises four groups, the Central and South American species of the subgenus *Tyrannus*, the western North American and Mexican species, the West Indian species and *T. tyrannus*, and the subgenus *Muscivora,* in which the two species are not only different in their RRVs from the members of the subgenus *Tyrannus* but also different from one another. (In this as in most other vocalizations, it is difficult to consider the forms found in *T. savana* because of their extreme simplicity.) Hereafter, for reasons of economy, I shall refer to the four groups as the tropical, western, eastern and *Muscivora* groups, respectively. Does the evidence provided by other displays tend to give us the same four groups?

Locomotory Hesitance Complex of Vocalizations

Within the eastern group a nice progression of related forms can be seen in at least the prolonged LHVs of *T. dominicensis* (which is relatively simple) to *T. caudifasciatus* (more complex) to *T. tyrannus* (complex in a similar way, and perhaps more extreme). At the simple end of this series, the form is similar to that of the prolonged LHV of *T. melancholicus,* and the prolonged forms of the other two species of the tropical group are also reasonably similar. Of the more prolonged forms characteristically used by males of the western group, those of *T. couchii* and *T. crassirostris* are quite similar, and there is an apparent relationship between some forms of the latter and the harsher variants of *T. vociferans.* The usual form of *T. vociferans,* however, is rather distinct and sounds like the *T. tyrannus* form — a convergence so superficial as to be without significance. This form of *T. vociferans* has units comprising two elements, one of which is a simple chevron. In these respects it resembles the usual male form of *T. verticalis* in which, however, both elements are simple chevrons. The form of *T. vociferans* resembles more closely the mirror image of the ILHV of *T. verticalis,* but the LHV of the latter species is in most respects unique in the genus, and is quite possibly a case of secondary simplification.

There is a general tendency for females of all species to have LHVs which are either always high-peaked or always end in high peaks, or to have an LHV variant which ends in high peaks. An example of the last is the AeV variant of the LHV often used by females of *T. tyrannus* when being approached by an aggressive bird. Likely the high peaks are a conservative feature throughout the genus, encoding either sex or a particular mood. Although the high peaks are thus a feature which cannot be used *per se* in infra-generic taxonomic comparisons, the different forms of the high peaked elements can be. Within the tropical group, for instance, the brief LHV forms characteristic of females are similar in several respects, and there is a different form characteristic of the females of the four species in the western group. Within the latter group, the forms of the females of the two Mexican species are especially similar. Thus a comparison of the LHV forms, whether those typical of males or of females, yields the same groups within the subgenus *Tyrannus* as are indicated by the RRV forms, and suggests the additional possibility that the two Mexican species are the most closely related pair of the western group. Also, the LHV forms of neither species of the *Muscivora* group show a relationship to any of the preceding groups, except for a slight and perhaps superficial resemblance between the LHV of males of *T. forficatus* and males of *T. verticalis.*

Compound Vocalizations

This display is not known and may not occur in the *Muscivora* group, and, as has been discussed in Chapter 9, CdVs are not homologous throughout the subgenus *Tyrannus.* In most cases too little is known about the CdV to make worthwhile comparisons — this is true, for instance, in the eastern group where the CdVs of the three species seem to be rather different from one another, and in the tropical group where the calls *thought* to be CdVs in *T. melancholicus* and *T. albogularis* are quite similar in form. Within the western group, the CdVs of *T. couchii* and *T. caudifasciatus* are similar in form and may be homologous, and the CdVs of the other two species are in both cases closely similar to the LHVs. Apparently the CdV may be a relatively new evolutionary "invention" of the subgenus *Tyrannus,* the characteristics of which were not clearly fixed prior to speciation within the subgenus. (This is not certain, but seems the more likely of two alternatives. Ambiguous situations are probably less common in the relatively continuous context afforded by open habitats, and the *Muscivora* species *could* have had CdVs and lost them.) What few similarities can be discerned from species to species do not conflict with our grouping according to other characteristics.

Chatter Vocalizations and Related Displays

In Chapter 9 I pointed out that a range of messages seems to have been available during the evolution of the CV, RV, ILHV and RHVs, and that it appears as if this range was divided in different ways during the evolution of each species. Thus none of these displays is strictly comparable from species to species, but the group as a whole probably is, and, as the division of message appears to affect most directly the relationship between the RV and ILHV while the CVs always kept a basic message of anxiety, the CVs are fairly comparable.

In the subgenus *Muscivora,* the data are adequate only for *T. forficatus,* and indicate no ILHV, a rather simple chevron shaped RV, and an enormously variable CV. In the subgenus *Tyrannus,* so far as is known, the CV is never so variable and there are usually two other vocalizations, usually distinguishable as ILHV and RV. Usually the CV of a species comprises (1) a series of highly variable, relatively prolonged units, or (2) a series of relatively invariable brief units. The three species studied in the eastern group have primarily the second sort, and *T. melancholicus,* the one species of the tropical group for which I have information, seems to be fairly similar. The four species of the western group have CVs which can be described as being of the first sort, with the possible exception of *T. crassirostris* which, in my relatively small sample, can only be described as intermediate with apparent indications of affinities to the first sort.

It is difficult to make a comparison of the other displays in this set. The only know chevron-shaped RVs occur in *T. verticalis* and *T. forficatus,* two species with quite variable CVs. The only known chevron-shaped ILHV occurs in *T. couchii,* which also has a highly variable CV. The RVs of *T. dominicensis and T. melancholicus* seem rather similar, but then so are their CVs; in this case the CVs are relatively simple and the RVs each comprise several elements. I cannot see that any taxonomic help can be gained here yet.

Attack Vocalizations

Where they are known, AtVs are invariably harsh and marked by a rapid and wide oscillation of frequency. This seems to be the case in a great many other birds I have observed, including many non-tyrannids, and may be a primitive, highly conservative characteristic.

Tumble Flights

Insufficient is known about the forms of this display in several species to make a useful comparison. Further, there is likely little to be gained by comparing the vocalizations used in the "tumble," since in most species they seem to be either the terminal portion of the RRV or something very closely related to it. Two species, however, make this vocalization more elaborate by introducing a series of brief, staccato sounds into it at approximately corresponding places. In both cases, most of the introduced sound is produced by a Wing Whirr, a display that occurs in the tumble of at least some other species. In both *T. verticalis* and *T. vociferans* this Wing Whirr is apparently invariable and is precisely timed with respect to the vocalization in at least its onset. The effect is to produce the staccato series at just the part of the vocalization in which *T. dominicensis* uses a series of brief vocalizations in its RRV. The resemblance may well be superficial; on the other hand, it may indicate that the occurrence of staccato sounds in that position is primitive. Until we know more about the Tumble Flights and their accompanying displays, however, this knowledge cannot help us understand the relationships of the species.

Other Non-vocal Displays

All of the other non-vocal displays seem to be much alike in all species where they are known. Whether this is because they have been relatively casually studied, or because they are relatively conservative is not fully clear, but the latter explanation seems more likely.

In summary, the various displays vary in their usefulness to us as indicators of taxonomic relationships. The RRVs and LHVs are the most useful, but some of the others are at least suggestive. In all cases, the displays which can be used support a division into a total of four groups which have been called tropical, western, eastern, and *Muscivora.*

Are these groups also evident from other kinds of data, or are other groupings indicated? There are few other characteristics known at present which could be used to identify species groups. One of these might be plumage color, and a division along these lines would place together the West Indian species, *T. tyrannus,* and the subgenus *Musci-*

vora on the one hand, and the western and tropical species on the other, with *T. crassirostris* sufficiently intermediate to require arbitrary assignment. The evidence of Chapter 10 stands against such an unlikely assortment. It was shown that most species which coincide in geographical range apparently avoid ecological overlap in large part by segregating into different habitats. These different habitats are characterized by different colors and shades of vegetation, and there is a nice correlation between the color and/or density of pigmentation, in particular of the dorsal plumage, of a species and the color and brilliance of its habitat. Such a proximate ecological correlation indicates a labile system and suggests that different species in similar habitats have probably converged in these characteristics. Convergence of this sort may have occurred in all of the four species groups suggested by the displays.

One might also attempt to recognize species groups within the genus on the basis of structural features (see Ridgway, 1907, for detailed descriptions), and could then recognize the possible subgenus *Muscivora* with its two relatively small species with extraordinarily long outer tail feathers. However striking the morphological similarities of these two species, the possibility of convergence is hard to rule out. Indeed, Meise (1949) feels that some morphological features (shapes of wing, tail, and bill) might indicate independent derivations from different *Tyrannus* lines. Yet, in view of the fact that there is no good hint in the case of either species of closer relation to any particular other group of species, the burden of proof would seem to lie in showing convergence. I am inclined to accept, at least for the present, *T. savana* and *T. forficatus* as being more closely related to one another than to any other species.

In the subgenus *Tyrannus* there is a considerable amount of variation in bill size and shape, but for the most part this is as great between subspecies as species, and the range of variation throughout the subgenus tends to be nearly continuous. A possible exception would be the unusually large bill of *T. cubensis*. But this large bill is apparently used to take prey that, for a kingbird, is also unusually large, and thus the bill also appears to be a proximate ecological adaptation. Although habitat segregation seems to be the rule among sympatric species of this genus on the mainland, it may have been harder to apply in the different evolutionary conditions of the West Indian archipelago. It appears as if the West Indian species are characterized by a partial habitat segregation, and that a greater degree of differentiation of feeding behavior took place in that line.

The West Indian line, in fact, is the most clearly differentiated in the subgenus *Tyrannus*. Zoogeographic considerations such as the small number of species suggest that avian invasions of the Greater Antilles have been fairly uncommon, and it is unlikely that more than one kingbird invasion was ever successful. *T. dominicensis, T. caudifasciatus,* and *T. tyrannus* are sufficiently alike in their display repertoires that they could all have come from one stock, and their relationships to one another are closer than their relationships to a member of any of the other proposed group with the possible exception of *T. dominicensis. T. dominicensis* is in many respects intermediate between the proposed eastern group and the proposed tropical group. Happily, however, it appears to be the conservative member of a series in which first *T. caudifasciatus* and then *T. tyrannus* show progressively more innovation in the repertoire.

In addition to its repertoire, the eastern line is apparently a unit with respect to its plumage adaptations. If *T. dominicensis* is related to the invading stock as its habitat, feeding behavior, and repertoire all suggest, then the stock must have lost its ability to produce a colorful plumage in the early stages of its adaptations to the island environments. This is borne out by all of the other members, since each is an inhabitant of denser vegetation than is *T. dominicensis;* each has a darker plumage than that species, but none has any appreciable amount of color — they have only darkened gray or brownish gray to black. This seems to be a line, then, in which the first adaptation (convergent with other lines in the genus) was to lose color in an open, brilliant environment with at least some degree of pale foliage. The line has further converged with the adaptations to denser habitats shown by other species by becoming more densely pigmented, even in the absence of cryptic coloration.

There is thus at least some support on the basis of structural features to recognize *Muscivora* as a group, and on the basis of zoogeography and plumage adaptations to recognize the eastern species group.

The species' repertoires suggest division of the remaining species into two groups, the western and the tropical. The mountainous, arid center of Mexico certainly has offered opportunities, especially during long-term fluctuations of aridity, for speciation around its edges, and it is not hard to imagine how the four western species could have originated from even a single invasion of a southern stock. The similarities of their four repertoires, and their differences from the known parts of the repertoires of kingbirds living in other arid regions, suggest common ancestry rather than convergence.

Possibly the Middle American range of *T. melancholicus* results from a second, more recent northward invasion. Such an hypothesis requires a barrier to easy dispersal, and the Panama water gap provided one until relatively recently. Evidence for the effectiveness of some such barrier can be found in the ranges of various tyrannids (e.g., *Pitangus sulphuratus, Myiarchus tyrannulus, Pyrocephalus rubinus, Myiodynastes maculatus, Camptostoma spp.,* and *Oncostoma spp.*), which show either a hiatus or evidence of secondary overlap in southern

Middle America. Thus considerations of historical zoogeography and other tyrannid genera help support the hypothesis that the western species group might have derived from a more tropical group following an early and isolated invasion of Middle America. That the repertoires of the four species now found there are similar to one another, and differ from those of other species living in other arid regions, helps suggest that common ancestry and not convergence has been involved.

Conclusions

The genus *Tyrannus* comprises 13 species which can be grouped as follows:

(1) Subgenus *Tyrannus*: (a) the "tropical" species group comprising *T. melancholicus, T. albogularis,* and *T. niveigularis,* (b) the "western" species group comprising *T. verticalis, T. vociferans, T. crassirostris,* and *T. couchii,* and (c) the "eastern" species group comprising *T. dominicensis, T. caudifasciatus, T. cubensis,* and *T. tyrannus.*

(2) Subgenus *Muscivora*: *T. forficatus* and *T. savana.*

Discussion

In addition to its recognition of species groups, the scheme presented above differs from most current taxonomic arrangements of these species in three ways.

(1) Subgenus *Muscivora.* It has been customary to recognize the two species included in this group as generically distinct from *Tyrannus.* On the whole, species with affinities to *Tyrannus* are all so closely related that it is very difficult to recognize generic boundaries in this part of the family, and this difficulty has usually been resolved by an oversplitting that has done much to obscure the closeness of relationships. The two species of *Muscivora* obviously share many structural adaptations, whether by convergence or not, and are more similar to one another than they are to the species of *Tyrannus.* Yet their relationship to *Tyrannus* is very close, and I think that one can argue that *all* of their special characteristics are proximate adaptations for fitting a kingbird to life in the more open savannahs.

First, let us consider their behavioral differences from the other species. Their vocal repertoires are apparently relatively small, the signals of *T. forficatus* are unusually variable, and the signals of *T. savana* are nearly all reduced to simple click-like sounds, or to bursts of clicks. In Chapter 9 I have argued that all of these features may be explicable on the basis of (a) unusually good opportunities for continuity of context offered by the ease with which individuals can be kept under observation by their conspecifics, and (b) a reduced sound environment of other species' calls. Given a pattern of communication that employs signals in contexts to generate meanings, these two aspects of the enviornment contribute to the effectiveness of context and thus reduce the load which the signals should carry, with the result that the signals need be relatively less complex and less distinct from one another.

A *second* behavioral peculiarity of these two species is in their foraging, which employs relatively much perching on the ground and which introduces the technique of hover-searching for prey above the vegetation. The latter is not a unique technique in the genus — in fact, it is not much different from flight gleaning — except perhaps in being applied to the search for prey flying above the general vegetative surface of the habitat. Members of the subgenus *Tyrannus* tend to accomplish the latter by perching in an exposed position and scanning the air around them. In relatively open savannahs the *Tyrannus* technique would be inefficient if perches were too scattered, and if prey kept close to the vegetation and was not easily visible against the sky. Feeding on the ground is likely an adaptation to a habitat in which there is an appreciable amount of open substrate (which, again, cannot be scanned efficiently from widespread perches). All kingbirds drop to the ground for prey occasionally, but most other habitats occupied by the genus offer less opportunity for this method.

The *third* behavioral peculiarity is the habit of males, even during the breeding season, of roosting communally. Communal roosting in the non-breeding season is known among at least some species of *Tyrannus* (e.g., *T. dominicensis*) as well as in both species of *Muscivora,* but the nightly relinquishing of territoriality by breeding males is apparently unique. It is not clear, however, that members of all populations of the two species have this habit, and in fact it seems as if it may only occur in relatively treeless portions of the species' ranges. If this is the case, if the communal roosting is primarily a response to the lack of sufficient suitable roosting trees, then it, too, can be explained as an adaptive response to the same features of the environment that lie behind the other behavioral adaptations.

In addition to behavioral peculiarities the two species of *Muscivora* share some structural features not typical of *Tyrannus.* The most important of these differences is the enormous elongation of their outer rectrices; also, it is noteworthy that both species are relatively small-bodied compared to most kingbirds. Both characteristics could easily be adaptations to the hovering method of foraging search. Hovering is an expensive form of flight in terms of energy requirements, and the bulk of a three-dimensional object reduces rapidly as the dimensions are reduced. Field observations indicate that the positions of the rectrices are constantly adjusted as a bird shifts position in hovering flight, or even as it attempts to remain in one position in the face of a variable wind. Field observations also suggest, however, that the long rectrices are useful for control not only when hovering, but also when actively pursuing flying prey.

In summary, the differences which characterize *Muscivora* are such as might be expected of a kingbird stock or stocks adapted to a habitat that is unusually open for kingbirds. The structural, plumage, and behavioral similarities between *Tyrannus* and *Muscivora* are extensive, and our classification would do better to recognize these than to recognize the ecologically oriented differences. Thus I hold the two species of *Muscivora* to constitute at most a species group within the genus *Tyrannus*. It is the most different of the species groups, and the only one broadly sympatric with members of other groups. For these reasons I have given it subgeneric status, and lumped the other three species groups as the second subgenus of the genus *Tyrannus*.

(2) *Tyrannus couchii*: This population, although originally described as a species, has usually been accorded only the status of a subspecies of *T. melancholicus*. Our studies of the Texas portion of the population reveal that its repertoire is not only fully distinctive at a species level of difference, but that it is in all ways characteristic of the western group, and is not similar to repertoires of *T. melancholicus* or other members of the tropical group. Were it not for the possiblity that there may be some intergradation of vocal characteristics (see Chapter 5) and of plumage characteristics (see Wetmore, 1943, and Miller *et al*, 1957) in the southern part of its range, suggesting interbreeding with *T. melancholicus*, there could be no question of its status as a member of a western superspecies. Presumably its evolution has been in geographic isolation from all other members of its subgenus (although more or less sympatric with the similarly isolated *T. forficatus*) and its present day contact with the northeastern populations of *T. melancholicus* is a secondary overlap, perhaps as recent as the introduction of domesticated grazing animals by the Spanish. If there is now interbreeding, it may be because there has never been selection against it. I should expect, though that such selection will act against hybrids as they appear if the hybrids use a mixture of the two distinct repertoires with all the imprecision and redundancy that such a mixing implies. Nonetheless, if interbreeding occurs, the populations are semi-species (see Mayr, 1963) and will be difficult to fit within a taxonomic scheme until natural selection decides the issue through permitting introgression or forcing increased intrinsic isolation. Because the repertoires are so different, and because they represent two different species groups, the latter possibility seems sufficiently likely that I should like to recognize the distinctiveness of the *couchii* population by according it specific status with a binomen.

T. couchii may well be what Mayr (1942, 1963) has called a "borderline case" between species and subspecies. In view of the relative constancy of the repertoire of *T. melancholicus* throughout its enormous range, it is surprising to think that a population with so different a repertoire as *T. couchii* may not be specifically distinct. Yet what this thought implies is merely that the two populations can and will interbreed in nature, not that such interbreeding is particularly successful. In fact, the coast of the Gulf of Mexico is a region in which there has been much recent active speciation; and introgressive overlaps, narrow borderline overlaps, narrow overlaps not characterized by interbreeding, and disjunct distributions are well known (for selected examples from birds see Selander, 1959, for jays; Selander, 1961, for grackles; and Dixon, 1955, for titmice; for a review of, and examples from other vertebrates see Blair, 1958). *Tyrannus forficatus* and *T. savana* may well be another pair of species for which isolation in the region of the northern part of the Gulf of Mexico has been important, and they do not yet have secondary geographic contact. It is interesting that a small number of *T. forficatus* winter each year in southern Florida rather than in Central America, for Florida is thought to have been one of the places of refuge for the northern populations of such pairs during times of climatic stress.

(3) *Tyrannus caudifasciatus*: The monotypic genus "*Tolmarchus*" is not recognized because its species, although in some respects a slightly unusual kingbird, is in other respects closely related to *T. dominicensis* and *T. tyrannus*. Most of the distinctive characteristics of the species may be the result of a need not to compete with *T. dominicensis* for food on the one hand, and to obtain intrinsic isolating mechanisms on the other. Thus *T. caudifasciatus* is partially *Myiarchus*-like in its habitat choice and foraging behavior, and has a distinctive RRV. The ecological modifications are not extreme, however, and the elements of the RRV show striking similarities with elements of the RRVs of *T. dominicensis* and *T. tyrannus* when examined as in fig. 9:1. There are no obviously important structural differences between *T. caudifasciatus* and the other species, other than that it is the only species lacking emarginated outer primaries in the male. This feature may be related to its usual flight habits, although I do not know how.

I should add that I am not alone in failing to recognize the genus "*Tolmarchus*." James Bond, who is much more intimately familiar with the West Indian avifauna than I am, has also ceased to recognize it (Bond, 1958), and Meise (1949) came independently to the same decision.

Finally, I should like to point out that I fully realize these three decisions are all to some degree arbitrary. I feel they have the advantage of making clearer the relationships among species that our present evidence suggests; I admit they have the disadvantage of not being conservative — a problem when we lack full knowledge of a situation. My own interests are very much in the relationships, and perhaps I tend to underrate the problems accruing to such changes in nomenclature. I hope this will not be permitted to eclipse what I feel is the most important systematic contribution of this study, namely that the knowledge of vocal repertoires and patterns of communication does reveal relationships between species that are phylogenetic.

SUMMARY

1. Flycatchers of the genus *Tyrannus* possess repertoires of signals with which they communicate under a variety of circumstances. These signals and their employment have been studied in the field in 12 of the 13 species, with the intent of (a) studying the communication process in these birds, (b) examining the ways in which the repertoire and the process can differ from species to species, (c) attempting to understand what governs such differences, and (d) investigating the phylogenetic relationships of the species. A detailed account of the pattern of communication is presented for *T. tyrannus;* less detailed accounts are given for each of the 11 remaining species.

2. Vocal signals have in all cases received the most intensive study. Because of their detailed structures and considerable variability, large samples have been tape recorded in the field and later analysed in the laboratory with a Sona-Graph. The following have been recognized, but are not necessarily fully distinct.

(a) Locomotory Hesitance Vocalization (LHV), used in various circumstances, from greetings to lone individuals patrolling, in which a tendency to locomote (usually to approach) appears to be to some degree inhibited.

(b) Incipient LHV (ILHV), used primarily in agonistic situations in which the communicator appears to be experiencing locomotory hesitancy and other tendencies.

(c) Repeated Vocalization (RV), used by birds that are more aggressive or more likely to be aggressive than are birds using the ILHV; commonly heard from guarding males, in bouts of countercalling, and in related circumstances.

(d) Repeated Hesitance and Simple Repeated Hesitance Vocalizations (RHV and SRHV), used by some species lacking distinguishable ILHV and RVs; these appear to encode the same general set of messages.

(e) Compound Vocalization (CdV), used almost exclusively by males in such activities as countercalling, when they appear to be defensive but inhibited.

(f) Attackee Vocalization (AeV), used by individuals responding to an attack, but not fleeing, or not yet fleeing.

(g) Attack Vocalization (AtV), used by attacking individuals.

(h) Regularly Repeated Vocalization (RRV), the most elaborate "song" type of vocalization, employed by males primarily in the predawn twilight, and by most species in the Tumble Flight display.

3. While vocalizations sound very different from species to species, non-vocal signals seem to be rather similar throughout the genus, and

are usually at least partially redundant to the vocalizations accompanying them. Nonetheless, they do affect different sensory systems, and they can add unique features, such as pointing, to the message of a vocalization.

(a) Tumble Flight (TF), a spectacular flight display given by males during or after tense agonistic situations.

(b) Wing Flutter (WFt), used with the LHV when expressing locomotory hesitance.

(c) Wing Flick (WFk), used by threatening individuals.

(d) Wing Whirr, a sound produced apparently by the primaries during flight under some agonistic circumstances (rare, not well understood).

(e) Tail Quiver, probably a usual accompaniment of the WFt.

(f) Tail Flick, the usual accompaniment of the WFk.

(g) Crouch, used by threatening individuals.

(h) Revealed Crown Patch (RCP) and Raised RCP (RRCP), used by threatening individuals.

(i) Crown Ruffled, a very common plumage signal, used in nearly all situations.

(j) Gape, used by an attacking individual.

(k) Bill Snap, used by an attacking individual.

4. The following basic types of message appear to be common to all species:

(a) inhibition of a tendency to locomote,

(b) anxiety over potentially disruptive situations,

(c) aggressiveness, usually with an indication of defensiveness or offensiveness,

(d) possibly fear, and

(e) identification of various sorts. The signals encoding these messages, and modifications and combinations of them, occur in many contexts and appear to overlap in function.

5. The signals of *T. tyrannus* and the ways in which they are used are examined with respect to seven social functions which must be mediated by signalling: attraction and repulsion of conspecifics, individual recognition, appeasement and reassurance, threat, providing environmental monitoring information to conspecifics, alerting, and the association of adults with dependent offspring. Taken alone, the available messages do not all relate in a direct fashion to the problems which must be solved, but when they are placed in all of their possible contexts, they generate a very large set of meanings. It is proposed that these meanings operate to fulfill the necessary functions, and the pattern of communicating found in *T. tyrannus* is discussed in the light of this hypothesis. Many meanings, however, are very difficult to observe, and in this study I attempted to circumvent this difficulty by

concentrating on the other essential features of communication events. That is, I studied communicators, signals, and contexts more than recipients, and attempted to infer messages from the behavior of the communicator. With a knowledge of messages, contexts, and some responses, it is possible to envisage the mode of operation of communication in this species, and to infer some of the other probable meanings.

6. A comparison of the repertoires and their employment in 12 species indicates that similar patterns of communicating exist throughout the genus. The various differences which have been discovered in the form and usage of signals from species to species appear to be explicable on the bases of differences in annual behavioral cycles, ecology, and phylogeny.

7. Particular signals are compared throughout the genus, revealing some patterning of the similarities and dissimilarities of form and message. This comparison is made more or less difficult in different cases because the repertoires of no two species have exactly the same divisions of the total set of messages. For example, in some species where the breadth of message carried by the CV and its variants is restricted (relative to the case in other species) the missing message possibilities are not lost but are part of the message set of the RV and/or other vocalizations. Further, at least the CdVs are shown to be not homologous in all species.

In each species, most of the recognizably different vocalizations are spanned by infrequent or common intermediates. Some vocalizations are continuously variable, while others comprise combinations of unlike elements and vary somewhat less. Some continuous sorts of modification (e.g., harshness) can be applied to most vocalizations, and signalling can also be varied continuously (e.g., in rate of repetition). All variations apparently encode modified messages. Those variations which make the accurate perception of signals more difficult create a need for redundancy and, in extreme cases, an increased availability of context.

8. The repertoires of females are smaller than those of males; and females, except when using the CV, display less than males in all situations. This may be due to the facts that (a) only one sex need advertise, and (b) the behavior of the female is much more predictable, much less likely to vacillate rapidly, than is that of the male.

9. Within the repertoires of at least *T. melancholicus* and *T. dominicensis* most vocalizations, at least to my ear, are relatively difficult to tell apart. For both species the breeding season is likely relatively long, and the birds may be able to sacrifice some distinctiveness of signals if there is a sufficiently strong selection pressure acting in a contrary direction. It is hypothesized that in the complex sound en-

vironment of these species it may be an advantage for all of the calls in the repertoire of each species to differ from the myriad of calls of other species in the same way.

10. Field observations supplemented from published material on all 13 species indicate that members of the genus occur in a wide range of habitats. Further, when two or more species are sympatric they usually segregate into different habitats. Throughout the genus there is an excellent correlation between color and darkness of plumage and the color of the environment. In some cases in the West Indies the segregation into distinct habitats appears to have gone less far than elsewhere, and there is a noticeable modification of foraging behavior in two species. Otherwise, the various species tend to employ the same method of foraging, based on the aerial pursuit of insect prey supplemented by some flight gleaning of invertebrates and fruits.

11. Characteristics of some of the vocalizations suggest that there are four species groups within the genus: four species in western North America and Mexico, three in Central and South America, four in the West Indies and eastern North America, plus the two species of the possible subgenus *Muscivora.* Of these, only the first two groups cannot be easily separated on the basis of other characteristics such as structure and plumage. The structural and behavioral differences of *Muscivora* seem to be adaptations to foraging in open savannahs, and the reduced and variable vocal repertoires of the subgenus may be explicable on the basis of the increased continuity of context and reduced sound environments of these habitats.

12. In addition to indicating that the 13 closely related species of *Tyrannus* appear to belong to four species groups, knowledge of the vocal repertoires leads to the recognition at a specific level of distinctness of the population *T. couchii.* This population is usually considered a subspecies of *T. melancholicus,* and there is some possibility that the two interbreed in a region of secondary contact. Nonetheless, the repertoire of *T. couchii* is not only as distinct as that of any other species, it is very different from the repertoire of *T. melancholicus* and is clearly related to the western species group.

GLOSSARY

The words below are of two kinds: first, terms of established and current usage within some field such as ethology or ecology, and second, terms for which I must stipulatively define my usages in this text. In this second category there are also two sorts of words: those much used in technical writing but which I wish to restrict (e.g., "signal") and those words of everyday occurrence for which I need a simple and unambiguous, often purely descriptive definition (e.g., "greeting"). In most cases where I have stipulated a definition it has been for the immediate end of making this book easier to understand, and does not imply that I wish to endow the term with a formal status in its restricted sense.

agonistic: having to do with attack and/or escape (see Scott and Frederickson, 1951); can refer to motivation, behavior, or even the situation which provokes the agonistic response. The term is synonymous with the term "hostile" of Moynihan (1955b), which is also widespread in the ethological literature.

anxious: a bird is described as being anxious when behaving *as if* it were uneasy, as if it were aware of an aversive or potentially aversive situation for which it had insufficient information to choose a response. (This definition is somewhat restrictive, and to that degree is stipulative.)

appeasement: a category of displays described by Moynihan (1955b) as being "designed" to prevent attack by directly reducing the actual and relative strength of another individual's attack tendency without provoking escape. Appeasement displays are a major feature in mutual overcoming of the individual distance phenomenon by two birds during pair formation. Such displays become less important and less common once the pair bond is formed, but reappear when extra-pair situations elicit high intensity agonistic responses. (See also *reassurance.*)

communication event: an event in which a communicator sends a signal and this signal is received by a different individual (a recipient). Any alert animal receives continuous information as it perceives the environment, and some of this information comes from other animals. For present purposes, however, I do not consider a signal to have passed between animals unless a display has been used; this is a more restrictive view of signals (and hence of communication) than is commonly used by other workers. (See also *display.*)

communicator: the sender of the signal (display) in a communication event.

context: the context of a display to a recipient comprises (a) simultaneous sensory inputs ("immediate context") and (b) a frame of reference based upon past experience, endocrine state, genetic program and the like ("historical context"); see Smith (1965) and an earlier discussion by Emlen (1960).

display: a vocalization, movement, posture, or chemical output which has been specially adapted in physical form or frequency to subserve social signal functions. (Definition adapted from Moynihan, 1960.)

element: as used herein, a component of a display or of a unit of a display. Not in all cases distinguishable from a unit. I intend the terms "element" and "unit" to be purely descriptive in this presentation, and have not hesitated to be arbitrary in the case of any display which might be composed of either elements or units. In the LHV of *T. tyrannus,* I have taken "kt-ter-ter" to be a unit (and "kt-ter" to be a shorter unit) of which "kt" and "ter" are elements; in the CV of the same species I have called each single burst of sound a unit for the simple reason that the sounds are at times used singly and are, in any event, nearly identical with one another. No theory of structure is implicit in this terminology. (See also *unit.*)

flight gleaning: obtaining prey or fruits by hovering near branches, twigs, and leaves, and plucking the food without perching. The food may be located either while hovering or while perched.

fluffed plumage: feathers partly erected so that the body appears very rounded with a smooth, unbroken outline (from Morris, 1956).

flycatching: the aerial pursuit and capture of insect prey.

floating population: a population of non-breeding individuals which is presumed to be present during the breeding season, its members not restricted to territories. It may account for the common sighting, in almost any territory, of occasional extra, non-aggressive individuals (the possibility exists that these are merely neighbors). Best evidence for the existence of such a population is from the replacement of killed individuals of the known breeders (see, for instance, the experimental work of Stewart and Aldrich, 1951).

greeting: I have used this word only to mean a situation in which two birds (usually members of a pair, or an adult and its offspring) come into close proximity and exchange displays. I do not intend it to have the status of a formal name of a type of behavior, since greetings under different circumstances may take quite different forms.

guarding: the state of an individual (usually a male) which perches alertly and persistently within sight of, and a short flying distance from, the nest, usually during the absence of its mate.

meaning: the meaning of a signal to a recipient is operationally defined as the response which the recipient chooses from all of the possible responses open to him (see Cherry, 1957, and Smith, 1965).

message: the information encoded in the signal which is descriptive of some aspect(s) of the central nervous state of the communicator (see Smith, 1965, and *in press*). These include both ephemeral and longer-term motivational states as well as limitations inherent in the repertoire of behavior typical of the species, sex, and individual.

mood: "the mood of an animal at any given moment is simply the state of all its drives at that time" (Russell and Russell, 1961).

noise: a dissonant sound; often (here) a brief burst of rapid and extensive frequency fluctuation or of "white noise."

pitch: the subjective impression of the highness or lowness of a sound, partly, but not wholly nor simply, determined by the frequency of the sound.

reassurance: in situations in which appeasement displays are used it is common for both interacting individuals to communicate, and often both use the same or closely similar displays. Desmond Morris has pointed out (pers. comm.) that it is not necessarily true that each individual is appeasing the other; one may be forestalling an attack of the other (appeasing) while the other is indicating that it will not likely make an attack (reassuring).

recipient: an individual, other than the communicator, receiving a signal in a communication event. (Through various sorts of feedback the communicator receives its own signal, but unless another individual also receives it there is no communication event; hence the term "recipient" to designate that important other individual.)

redundancy: a characteristic of signals or parts of signals which convey the same information. The function of redundancy is to help ensure that the recipient gets the message in a "noisy" environment; if the signals or their parts are sufficiently redundant, he need only receive them in part to be able to predict what the entire message was. (see explanation by Moles, 1963).

ritualization: "the evolutionary process responsible for the existence of inter- and intra-specific signalling movements" (Blest, 1961); that is, the process by which displays become stereotyped and (to varying degrees) distinct.

ruffled plumage: feathers fully erected and the body, although rounded, has a ragged appearance with a broken outline (from Morris, 1956).

signal: that which encodes the message and is transmitted by the communicator in the event of a communication. The signal, as the term is employed here, is usually what ethologists refer to as a "display" (q.v.). Unfortunately, it is not always possible to know if evolutionary modification ("ritualization," q.v.) has in fact taken place, but one can usefully deal with that set of actions which includes only displays and acts which are functionally very like displays.

In using "signal" to refer only to displays and events which are very like them, I am restricting the term to a fraction of what it is used to cover in most communication theory. This is intended purely as a convenience, and I should not do it were I discussing perception in general. For present purposes the alternative, extending the term "display," is worse because it involves hidden assumptions about evolutionary histories.

sleeked plumage: feathers fully depressed against the body giving it a slim appearance (from Morris, 1956).

social: an *interaction* is "social" when it involves more than one individual. This is a broader employment of the term than is favored by some authors, but is essentially the usage of Tinbergen (1953).

supplant: to take the perch of another individual; occurs in a form of aggressive encounter in which the aggressor displaces the aggressee, usually without a fight, and takes its place.

tendency: a term used to replace more ambiguous words such as "drive" when referring to the existence of causal factors acting within an animal to produce certain behavior; it implies that an individual's behavior would be predictable from a knowledge of these causal factors if an observer could know their changing strengths and interactions. Thus, e.g., a bird with an aggressive tendency may attack if the tendency is sufficiently strong and does not become inhibited through the action of other tendencies (see Hinde, 1955).

territory: During this study I adhered to Noble's (1939) definition: any defended area. Very often, however, little or no defence was seen, and I concluded that territory varied rapidly within a wide range. Weeden (1965), faced in a non-tyrannid with a problem which was at least partly comparable, developed measurements of "activity space" which should probably be applied to the nest-centered areas occupied by kingbirds.

unit: as used herein, an entire display, or some portion of a display which is repeated in series. (See *element.*)

zoosemiotics: the study of animal communication (see discussion by Sebeok, 1965).

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